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Bulletin British Museum (Natural History)

Zoology Series

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(NATURAL HISTORY)
31 MAY 1989
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VOLUME 55 NUMBER 1 25 MAY 1989

The *Bulletin of the British Museum of Natural History*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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BRITISH MUSEUM
PUBLICATIONS
ISSUED
31 MAY 1989
SALES OFFICE
NATURAL HISTORY

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

© British Museum (Natural History), 1989

ISBN 0 565 05045 1
ISSN 0007 – 1498

Zoology Series
Vol 55 No 1 pp 1 – 121

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 25 May 1989

Typeset by J & L Composition, Filey, North Yorkshire
Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

Bull. Br. Mus. nat. Hist. (Zool.) 55(1): 1–9 Issued 25 May 1989

Structure and taxonomy of the genus *Delosina* Wiesner, 1931 (Protozoa: Foraminiferida)

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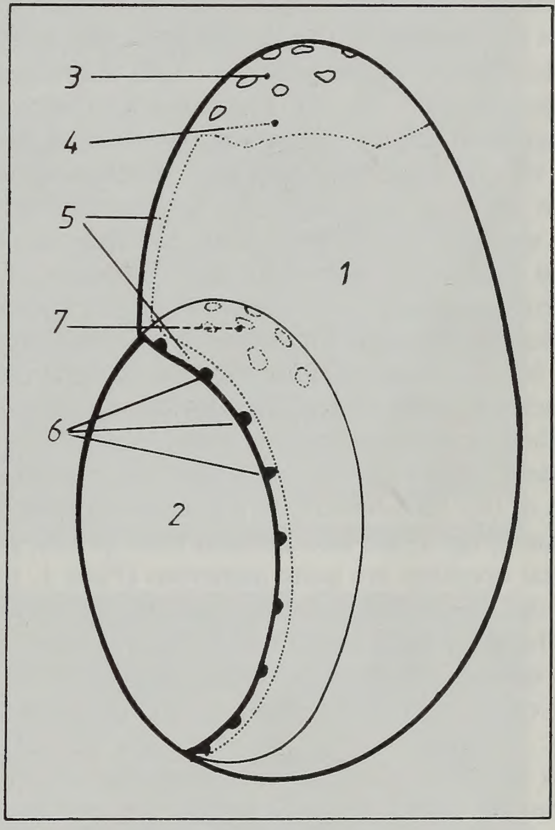
Synopsis. The systematic position of the genus *Delosina* is reassessed in the light of structural and morphological observations. The non-lamellar wall structure and a new type of wall ultra-structure leads to the proposal of a new, separate suborder, the Delosinina. The species *Delosina complexa*, *D. complanata*, *D. sutilis* and *D. wiesneri* are emended and lectotypes are designated and described. *D. polymorphinoides* is synonymised with *D. complexa*.

INTRODUCTION

In 1907, Sidebottom described a new species, *Polymorphina (?) complexa*, expressing much puzzlement as to the true affiliation of this unusual taxon. After the initial description, specimens more or less referable to this form were found in a variety of localities, but always as a rare species. Sidebottom corresponded with Earland about the possible relationships of this species (*fide* Earland, 1934, p. 125), from which it appears that Sidebottom contemplated the erection of a new genus, *Delosina*, to accommodate his *Polymorphina (?) complexa*. He never came to publish this because of the major difficulties he encountered in handling this species, the specimens being small, fragile, and very transparent. Heron-Allen and Earland (1915) established the existence of secondary apertures along the sutures, which gave a 'postage stamp fracture' in broken specimens. Wiesner (1931) found a number of specimens in the material gathered by the German Antarctic Expedition and, by a happy coincidence, proposed the name *Delosina* as a new genus to accommodate what he considered to be the *Polymorphina (?) complexa* of Sidebottom (later studies showed the *Delosina complexa* sensu Wiesner to be two different species). Because of the fact that his specimens were substantially larger, he was able to demonstrate the existence of a canal underlying the sutures, thus showing that the sutural apertures do not communicate directly with the chamber lumen (see Textfig. 1 for a clarification of the anatomical terms used). While working on the material gathered by the *Discovery* and the *William Scoresby*, Earland (1934) revised the genus. Besides this new material he also had the original material of Sidebottom at his disposal and had received the figured specimens of Wiesner. Revising and comparing all this material he erected four more species; *Delosina complanata*, *D. polymorphinoides*, *D. sutilis*, and *D. wiesneri*. Earland also suggested, tentatively, to remove *Delosina* from the Polymorphinidae to the Buliminidae, because he had observed what seemed to be a loop-shaped aperture in the proloculus in one of the sections. He expressed serious doubts, however, about the validity of this move. Cushman (1948) followed Earland's suggestion and placed *Delosina* in the Uvigerininae; Buliminidae. Parr (1950) preferred to erect a separate family for the genus, the Delosinidae. This family was retained by Loeblich and Tappan (1964); they placed it in the Cassidulinacea on account of its possession of an optically granular wall, close to the Fursenkoininae because of a certain resemblance between *Delosina* and *Virgulinella*. Haynes (1981) kept *Delosina* in the Buliminidae, closely allied with *Virgulinella*. In the latest classification, Loeblich and Tappan (1984) raised the Delosinidae to the rank of superfamily, comprising the Caucasinidae (Baggatellinae and Caucasininae), the Tremachoridae and the Delosinidae, all within the suborder Rotaliina. Until today, all changes in the taxonomic position of *Delosina* have been based on the gross morphology. The aim of this study is to shed some light



Textfig. 1 Anatomy of *Delosina*. 1. Ultimate chamber. 2. Penultimate chamber. 3. Trematophore. 4. The cup-shaped feature underlying the trematophore. 5. Subsutural tube, which is a continuation of (4). 6. Sutural openings. 7. The foraminal trematophore, which is entirely contained in the lumen of the next chamber.

on the true affiliation of *Delosina* by means of detailed observations on its morphology and structure.

Material & Methods

A number of specimens of *Delosina complexa*, whole and sectioned, were observed in the scanning electron microscope. Sections were made following Grønlund and Hansen (1976) and Morkhoven (1958). The sectioned specimens originate from the Arafura Sea, Station 501 of the Danish Galathea Expedition. All specimens housed in the British Museum (Natural History) were studied.

OBSERVATIONS

Observations on intact specimens clearly show the existence of the sutural apertures, which in some cases may be so small as to escape notice under the stereo-microscope (Plate 2, fig. 3). The cribrate aperture, or trematophore, is seen to consist of a series of openings in a rather irregular area between the apex of the ultimate chamber and the sutural line most close to this apex (Plate 1, fig. 2). The openings themselves are quite irregular in outline. In section they show ragged edges (Plate 2, fig. 2), suggesting they may have been formed by resorption rather than being built. Since no veneer can be seen and since the edges, in section, are irregular, it seems likely that they were formed by the dissolution of calcite, starting from, say the pores, instead of being left open during the calcification process. The pores in the wall are minute (Plate 1, figs 3, 4) and most of the time irregular in shape. Some specimens have a surprising low density of pores. The sections show very clearly the subsutural tubes (Plate 1, figs 1, 5, 6; Plate 2, figs 1, 3, 4), including the cup-shaped prolongation of this tube underlying the trematophore (Plate 1, fig. 4; Plate 2, fig. 1; see also Earland 1934, p. 126, point iv). The sutural openings are quite numerous (Plate 1, fig. 6); in contrast, the number of openings from the tube towards the chamber lumen is very low (Plate 2, fig. 4). A few of these openings towards the lumen can also be seen in the broken specimen of Wiesner (1931, Plate 21, fig. 256; slide BMNH ZF 3226).

From a structural point of view some remarkable observations can be made. The wall structure is non-lamellar. It consists of small, blocky crystalline elements, somewhat reminiscent of the microgranular type of structure but differing from the latter in being irregular (Plate 2, fig. 6). This is a new type of wall structure, it has no known equivalent in the calcite-secreting Foraminifera.

It is worth noting that the monolamellar taxa in the Rotaliina, i.e. the Nodosariidae, show a radial wall structure, both optically and ultrastructurally (Grønlund and Hansen, 1976).

Secondary lamination is absent (Plate 1, fig. 3; Plate 2, figs 1, 5). When a new chamber is added, the remainder of the test is not covered by an extra layer of calcite. This is, again, a fundamental deviation from the general pattern within the Rotaliina. The few taxa that exhibit the lack of secondary lamination (one species in the Nodosariidae and a few in the very primitive Syzraniidae, which are now classified in the Lagenina) have a radial wall when viewed under polarized light.

Following the rationale behind the latest classification scheme (Loeblich and Tappan, 1984), *Delosina* should be separated from all the other perforate calcitic Foraminifera. I therefore propose to erect a new suborder, the Delosinina.

Although originally included in the Delosinacea, I do not consider the Caucasinidae and the Tremachoridae to be member taxa of the Delosinina. The genus *Caucasina* possesses a toothplate, a bilamellar granular type of wall structure and shows secondary lamination. These features suffice to put it in the Buliminacea. I do not consider the optical nature of the wall structure to be a character sufficient to warrant the separation of families. The genus *Tremachora* remains an enigmatic taxon. Since no data are available as to the internal morphology nor the ultrastructure of the wall, I prefer to consider the taxonomic position of *Tremachora* as uncertain until more information becomes available.

A puzzling fact concerning *Delosina* is the apparent absence of a geological record. Although it shows some advanced morphological features, the absence of secondary lamination and especially the wall structure points towards a long geological history. In the scheme proposed by Hansen (1979), *Delosina* would belong somewhere between the micro-granular group and the group secreting optically orientated calcite, two groups with a substantial geological record. A possible reason for the absence of *Delosina* in the fossil record can be found in the very fragility of the test. The fact that the successive chambers are joined only by the rims of the subsutural tubes (Plate 1, fig. 6) without subsequent reinforcing secondary lamination results in a very fragile test (the specimens are difficult to handle, they break easily, even when using a brush carefully). It is doubtful that the tests of *Delosina* would survive the rough average taphonomical treatment, especially since *Delosina* occurs in the more shallow water zones.

SYSTEMATICS

Order: FORAMINIFERIDA Eichwald, 1830

Suborder: DELOSININA subord. nov.

Test multilocular, chambers arranged in coils; chambers simple; wall calcareous, composed of very small, blocky, irregular crystalline units, monolamellar; secondary lamination absent.

Family: DELOSINIDAE Parr, 1950

Test triserial, may become biserial, or biserial throughout; wall perforate, appearing optically indistinctly granular; aperture a trematophore which may be absent; sutures with sutural openings which give access to a subsutural tube.

Genus: *DELOSINA* Wiesner, 1931

TYPE SPECIES. *Polymorphina (?) complexa* Sidebottom, 1907

DESCRIPTION. Test free, elongate, or extremely inflated, rounded in section, may be laterally compressed. Chambers arranged in coils, usually triserial, may become biserial, or biserial throughout. Chambers embracing, usually starting

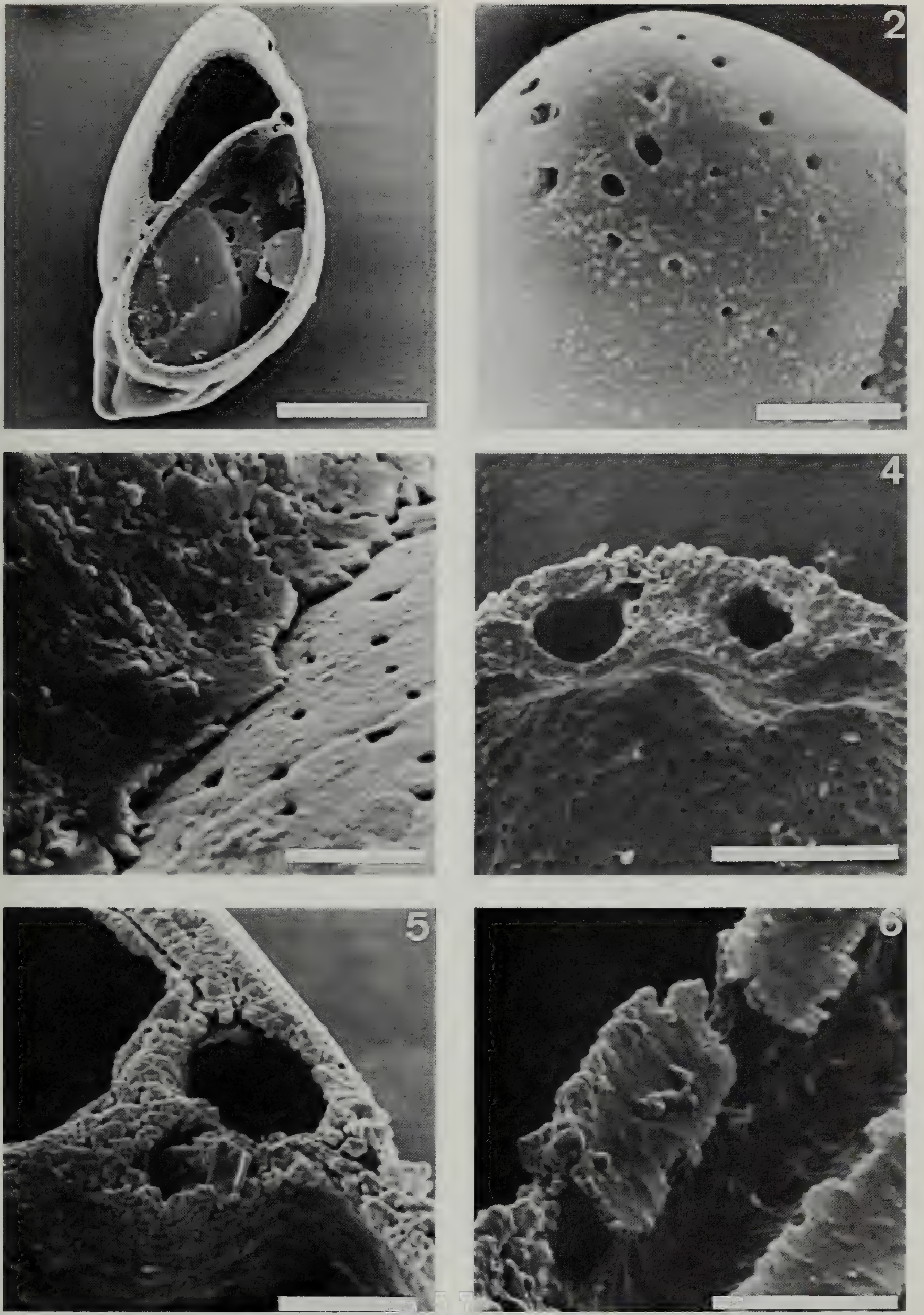


Plate 1 *Delosina complexa*, Arafura Sea. Fig. 1. A partially sectioned specimen, showing the trematophore, subsutural tubes, sutural openings and the general disposition of the chambers. Scale bar: 100 µm. Fig. 2. A close-up of the trematophore. Note the larger openings surrounded by a series of smaller openings lying in a loop around the apex. Scale bar: 20 µm. Fig. 3. Internal view showing how a chamber joins a previous one without secreting extra layers of calcite, as the line of contact and the pores of the previous chamber clearly demonstrates. Scale bar: 3 µm. Fig. 4. Part of the cup-shaped feature underlying the trematophore. Note that this cup is not a chamberlet but an enlarging of the subsutural tube. Scale bar: 20 µm. Fig. 5. A close-up of Fig. 1, showing the subsutural tubes of ultimate and penultimate chamber. Scale bar: 10 µm. Fig. 6. A view of the inside of the subsutural tube, seen from the lumen side, showing the sutural openings and the constructional relationship between the tube and the wall of the previous chambers. Scale bar: 20 µm.

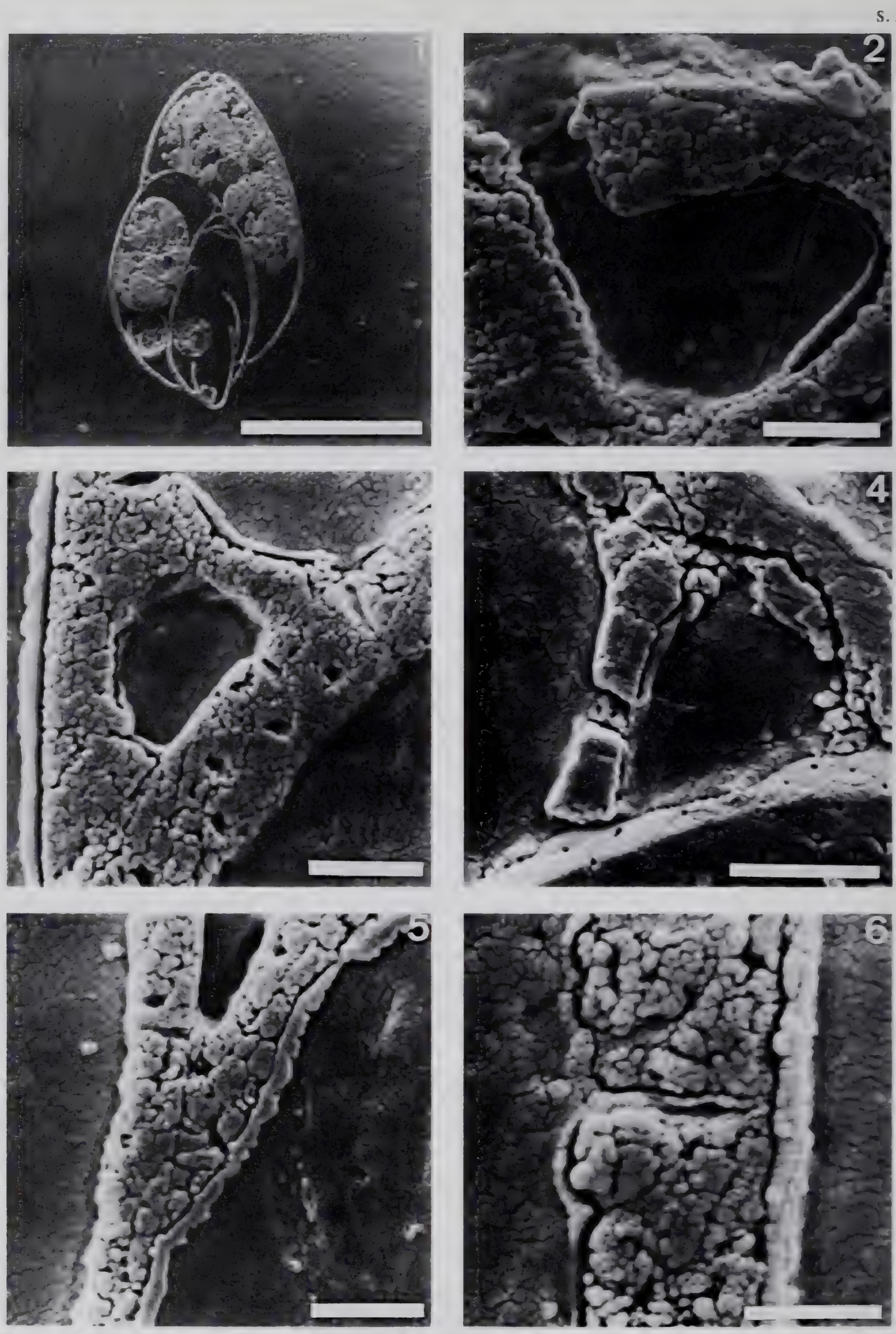


Plate 2 *Delosina complexa*, Arafura Sea. Etched sections. Fig. 1. A general view, showing the disposition of the chambers, subsutural tubes and cup-shaped features underlying the trematophore. Scale bar: 200 µm. Fig. 2. A section through the trematophore. Note the coarse edges on the opening. Scale bar: 5 µm. Fig. 3. A close-up of the contact between two chambers, with a subsutural tube. Note that no septal flap is formed. Note also the absence of structure in the walls, including the subsutural tube. Scale bar: 5 µm. Fig. 4. A subsutural tube with an opening towards the lumen. Scale bar: 10 µm. Fig. 5. Contact between two chambers, showing the absence of secondary lamination. Scale bar: 5 µm. Fig. 6. A close-up of the ultrastructure of the wall, showing it to be composed of very small, blocky crystal units, irregularly placed against each other, in contrast with the regular arrangement seen in microgranular walls. Scale bar: 3 µm.

very close to the proloculus, may become more evolute, especially when becoming biserial. Sutures somewhat marked, lying at the edge of a depression where the chambers adjoin, punctured by a series of small openings, the secondary apertures, which give access to a subsutural tube. The aperture, which may be absent, is a trematophore lying at the apex of the chamber, extending down to the nearest suture. Inside the chamber the trematophore is isolated from the lumen by a cup-shaped feature, which itself is continuous with the subsutural tube (the cup-shaped feature is absent if the trematophore is lacking). The subsutural tube allows some access to the chamber lumen through a low number of openings. Ornamentation is absent.

Delosina complexa **(Sidebottom)**

Pl. 1, figs 1–6; Pl. 2, figs 1–6; Pl. 3, figs 1–2.

1907 *Polymorphina (?) complexa* Sidebottom: (*pars*), 16, textfigs 3–7, Pl. 51, figs 1–7 (only).
1915 *Polymorphina complexa* Sidebottom; Heron-Allen and Earland: 673–674, Pl. 51, figs 1–3.
1918 *Polymorphina complexa* Sidebottom; Sidebottom: 145, Pl. 5, figs 13–14.
non 1931 *Delosina complexa* (Sidebottom); Wiesner: 123, Pl. 21, figs 254–256.
1934 *Delosina complexa* (Sidebottom); Earland: 127–128, not illustrated.
1934 *Delosina polymorphinoides* Earland: 128–129, not illustrated.
1939 *Delosina complexa* (Sidebottom); Heron-Allen and Earland: 177, not illustrated.

MATERIAL. BMNH. 3 slides, Delos, Sidebottom collection (*pars*). 1 slide, Delos, Heron-Allen and Earland collection. 1 slide, The Lido, Venice, Italy, Heron-Allen and Earland collection. 1 slide, Bay of Naples, Italy (labelled *Polymorphina complanata*), Heron-Allen and Earland collection. BMNH 1969:4:30:112:cell 63, Ebro Delta, Spain, Scrutton collection. BMNH 1965:11:92 and 93, Torbay, S. Devon, England, Milton collection (*pars*), and 1965:11:25:91, ibid., id. (labelled *Polymorphina complanata*). 1 slide, Baron Heads, Victoria, Australia (labelled *P. complanata*), *dedit* Parr. BMNH 1955:10:21:110, Kerimba Archipelago, Heron-Allen and Earland collection (labelled SYNTYPE *Delosina polymorphinoides*). Slide TS 641, cell 73 (*pars*), South Orkneys, *Discovery* station 170, Heron-Allen and Earland collection. Specimens from the Arafura Sea, *Galathea* station 501, Zoological Museum, Copenhagen, Denmark. Specimens from the Ebro Delta, Spain, J. W. Murray coll., Geologisk Central Institut, Copenhagen, Denmark.

LECTOTYPE. BMNH ZF 4725, Delos, Greece. Figured in Plate 3, figs 1, 2.

DESCRIPTION. Test free, slender, ovate, maximum width slightly above the middle of the test, triserial; chambers embracing, ellipsoid drawn out, well rounded, sutures somewhat depressed, sharply delineated, gently curved, punctured by sutural apertures which allow immediate access to a subsutural tube which ends in a cup-shaped feature underlying the trematophore-like aperture at the apex of the chamber, tube and sutural openings barely visible in the light-microscope (150 X); trematophore a series of coarse perforations running up from the sutural base almost to the apex of the chamber; wall calcareous, hyaline, very finely perforate, optically granular. Lectotype with 7 chambers; test length: 405 μm, width: 284 μm.

REMARKS. Sidebottom's *P. (?) complexa* contained two discrete species. The specimens figured by Sidebottom (1907, Pl. 51, figs 8, 9) were renamed by Earland (1934) as *Delosina complanata*.

It seems that a clear dimorphism is present in this species. The individuals with a very small proloculus answer the description of the lectotype; individuals with a larger proloculus appear as being somewhat compressed laterally, and the last chamber(s) show a tendency of becoming rectilinear.

The only specimen referable to *Delosina polymorphinoides* Earland, 1934, seems to be a good *D. complexa*, only with more inflated chambers. Since different degrees of inflation are present in the material, and since the specimens intergrade freely, I consider *D. polymorphinoides* to be the same species as *D. complexa*.

According to Dr Hounsome, Manchester Museum, no specimens of *Polymorphina complexa* are present in the collections of that Museum, thus confirming Earland's statement that Sidebottom had sent him all his material (Earland 1934, p. 125).

DISTRIBUTION. Recent. North Sea, Mediterranean, Indo-Pacific and Antarctic province (see Textfig. 2).

Delosina complanata **Earland**

Pl. 3, figs 3–4.

1907 *Polymorphina (?) complexa* Sidebottom: (*pars*), 16, Pl. 51, figs. 8–9 only.
1916 *Polymorphina complexa* Sidebottom; Heron-Allen and Earland: 48, Pl. 8, figs. 5–7.
1934 *Delosina complanata* Earland: 128, not illustrated.

MATERIAL. BMNH. Slides from Delos, Greece (labelled *P. complexa*, *pars*) Sidebottom collection. Slide TS 512, cell 42 (*pars*), *William Scoresby*. BMNH 1965:11:25:92 and 93, Torbay, S. Devon, England, Milton collection (*pars*). BMNH 1955:10:25:290, Cornwall, England (labelled SYNTYPE), Heron-Allen and Earland collection.

LECTOTYPE. BMNH 1955:10:25:290. Figured in Plate 3, figs 3–4.

DESCRIPTION. Test free, elongate, sides almost parallel, gently rounded, chambers opposite, giving a compressed appearance, coiling axis may be gently curved; chambers elongate, well rounded; sutures sharply marked at the contact between the chambers, somewhat undulate, punctured by small openings, the sutural apertures which give access to the subsutural tube, this tube can be seen as a faint extra line running parallel with the suture, thickening at the top of the previous chamber, giving the impression of a very small lip; trematophore and the cup-shaped feature are absent; wall calcareous, hyaline, finely perforate. Lectotype, test length: 335 μm, width: 167 μm.

REMARKS. Differs from the megalospheric specimens of *D. complexa* in having no trematophore, and in being biserial throughout.

DISTRIBUTION. Recent. North Sea, Mediterranean and Falklands (see Textfig. 2).

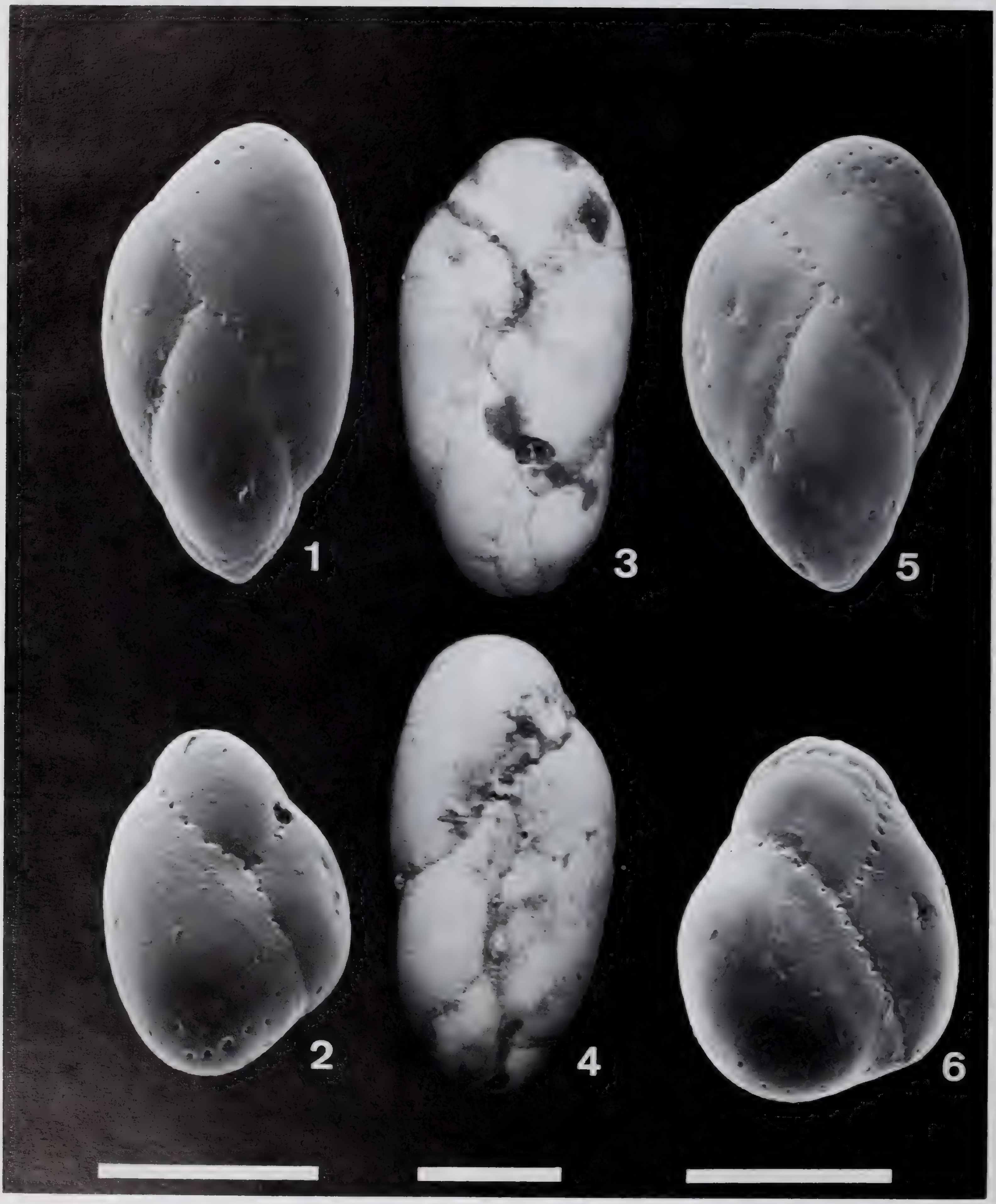


Plate 3 Figs 1, 2. Lectotype of *Delosina complexa* (Sidebottom), Delos, Greece. Scale bar: 200 µm. Figs 3, 4. Lectotype of *Delosina complanata* Earland, Cornwall, England. Scale bar: 100 µm. Figs 5, 6. Lectotype of *Delosina sutilis* Earland, South Orkneys. Scale bar: 500 µm.

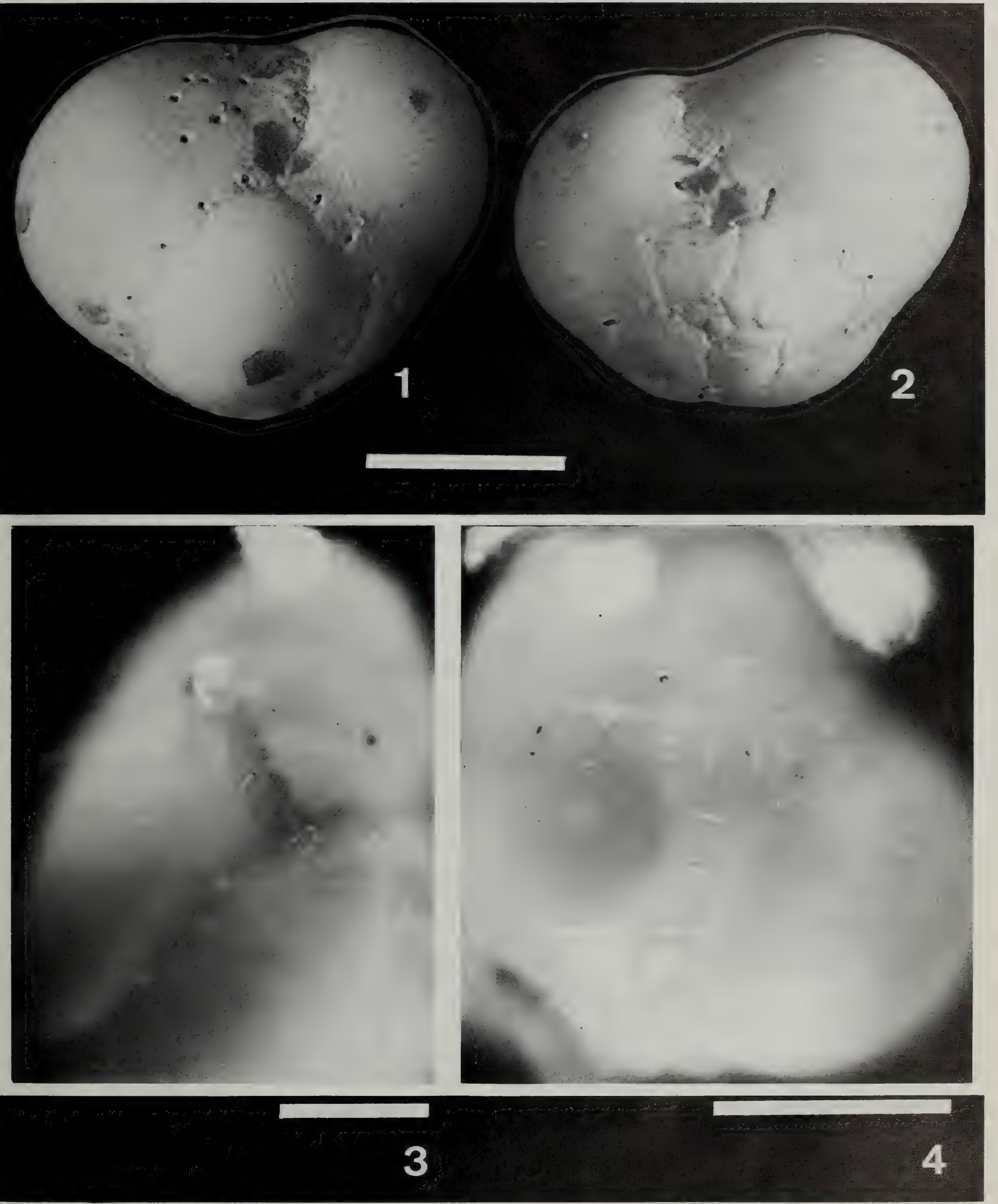
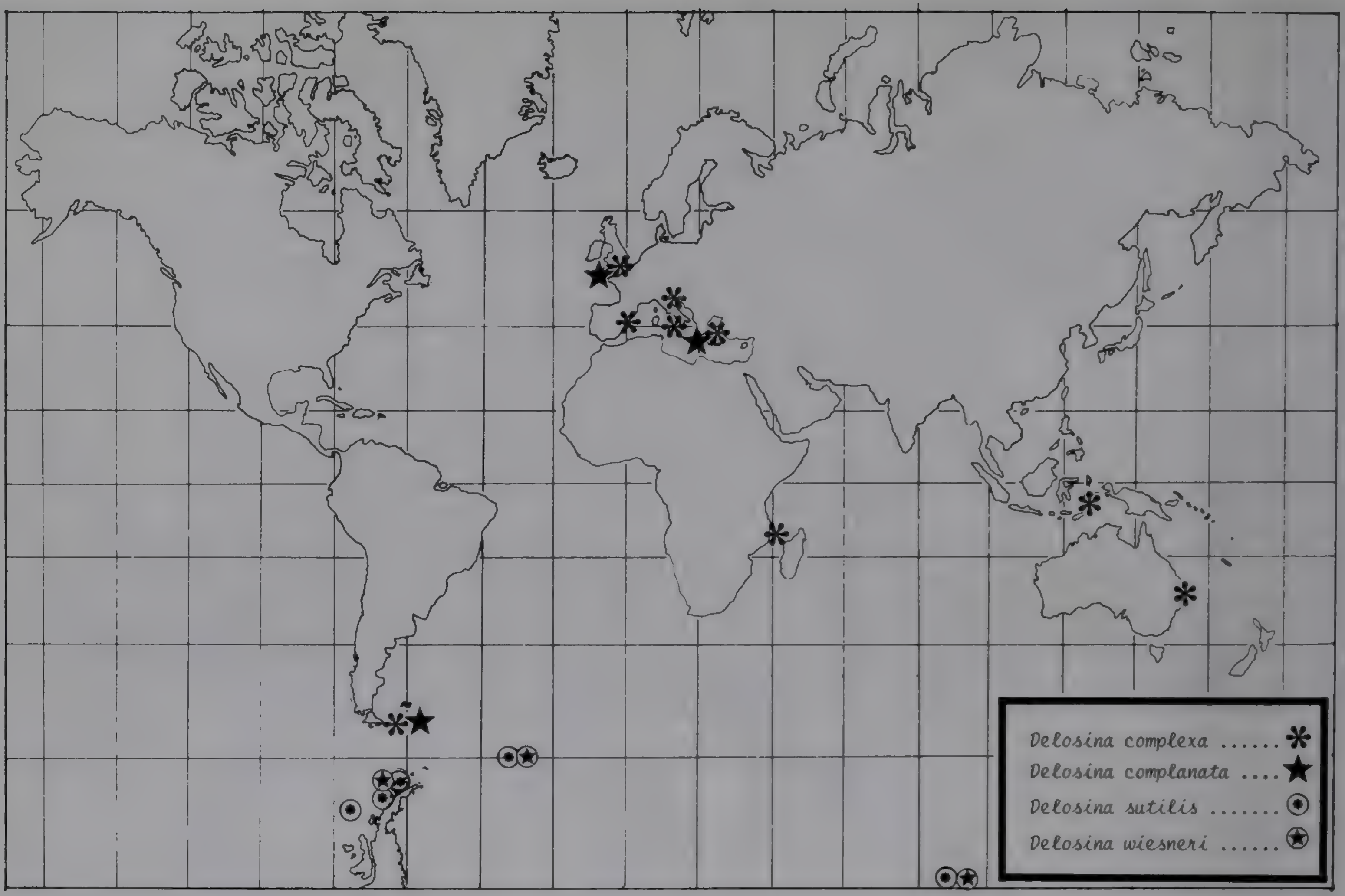


Plate 4 Figs 1, 2. Lectotype of *Delosina wiesneri* Earland, South Sandwich Islands. Scale bar: 200 µm. Fig. 3. Light microscope photograph of *Delosina sutilis*, immersed, showing the small canals which connect the sutural openings with the subsutural tube. Scale bar: 200 µm. Fig. 4. Light microscope photograph of *Delosina wiesneri*, immersed, neatly showing the almost dendritic pattern of the canals between subsutural tubes and sutural openings. Scale bar: 200 µm.


Delosina complexa ...... *
Delosina complanata .... ★
Delosina sutilis ...... ⊙
Delosina wiesneri ...... ⊛

Textfig. 2 The geographical distribution of *Delosina*.

Delosina sutilis Earland

Pl. 3, figs 5–6, Pl. 4, fig. 3.

1931 *Delosina complexa* (Sidebottom); Wiesner: (*pars*), 123, Pl. 21, fig. 254 only.
1934 *Delosina sutilis* Earland: 129, Pl. 5, figs 1–8.

MATERIAL. BMNH. Slides ZF 3229, ZF 3228, South Shetlands, *Discovery*, and 3 balsam embedded specimens, Heron-Allen and Earland collection. BMNH 1955:11:3:258, a balsam embedded section. Slides TS 627, cell 61; TS 641; cell 73 (*pars*); TS 642, cell 75; TS 660, cell 69 (*pars*); all type slides *Discovery*, Heron-Allen and Earland collection. BMNH ZF 3226 (*pars*), out of Kaiser Wilhelm's Land, Antarctica, Wiesner collection.

LECTOTYPE. BMNH ZF 4726, South Orkneys. Figured in Plate 3, figs 5–6.

DESCRIPTION. Test free, elongate, large, ovate, greatest width around the middle of the test, triserial; chambers large, somewhat inflated, embracing; sutures at the edge of a band-like depression between the chambers, gently curved, punctured by comparatively small sutural openings which give access to a narrow, gently curved canal which opens into the subsutural tube, forming a branching-like network; aperture a prominent trematophore; wall calcareous, semi-opaque, very finely perforate. Lectotype, test length: 1130 μm, width 720 μm.

REMARKS. Differs from *D. complexa* in being substantially larger and in possessing a band-like depression between the chambers in which canals connect the sutural openings with the subsutural tube.

DISTRIBUTION. Recent. Antarctic province, (see Textfig. 2).

Delosina wiesneri Earland

Pl. 4, figs 1, 2, 4.

1931 *Delosina complexa* (Sidebottom); Wiesner: (*pars*), 123, Pl. 21, figs 255–256 only.
1934 *Delosina wiesneri* Earland: 130, Pl. 5, figs 9–15.

MATERIAL. BMNH. Slides ZF 3227, ZF 3225, South Sandwich Isles, resp. South Orkneys, *Discovery*. Slides TS 660, cell 69 (*pars*), *Discovery*; Heron-Allen and Earland collection. Slide ZF 3226, off Kaiser Wilhelm's Land, Antarctica (*pars*), Wiesner collection.

LECTOTYPE. BMNH ZF 3227a, South Sandwich Islands. Figured in Plate 4, figs 1–2.

DESCRIPTION. Test free, stout, almost twice as broad as long, triserial; chambers extremely inflated, almost spherical, somewhat embracing; sutures at the edge of a band-like depression between the chambers, punctured by very small sutural openings which are the outer ends of canals, which gently curve away from the subsutural tube; the trematophore is very irregular, a few coarse punctations in an area usually lying close to the suture between the ultimate and the penultimate chamber; wall calcareous, semi-opaque, very finely perforate. Lectotype, test length: 310 μm, width: 400 μm.

REMARKS. Somewhat similar to *D. sutilis*, but differing in being extremely inflated and in possessing a very irregular and often obscure trematophore.

DISTRIBUTION. Recent. Antarctic province (see Textfig. 2).

ACKNOWLEDGEMENTS. I wish to thank Dr C. G. Adams and Dr J. E. Whittaker for their hospitality and generous help during my stay at the British Museum (Natural History). I wish to express my gratitude to Dr Whittaker for the great pains he took in photographing the lectotypes and the immersed specimens. I gratefully acknowledge a scholarship granted by the Belgian–Danish Cultural Agreement allowing me to carry out, *inter alia*, the ultrastructural part of the research here presented. I wish to thank Dr H. J. Hansen and Mr J. F. Nielsen for their hospitality and encouragement during my stay at the Geological Institute of the University of Copenhagen, Denmark.

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Manuscript accepted for publication 10 June 1987

Bull. Br. Mus. nat. Hist (Zool.) **55**(1): 11–17 Issued 25 May 1989

Morphology and morphogenesis of *Parakahliella haideri* nov. spec. (Ciliophora, Hypotrichida)

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SYNOPSIS. A description of the morphology and the morphogenesis of the hypotrichous soil ciliate *Parakahliella haideri* nov. spec. is given. This species differs from its congeners by its possession of a single left marginal row. The morphogenesis of both the ventral and dorsal infraciliature proceeds in a very similar way to that of the type-species *P. macrostoma*, indicating congenerity of these species. Thus, the diagnosis of *Parakahliella* is emended to include species with only 1 left marginal row.

INTRODUCTION

Recently, the kahliellid genus *Parakahliella* with *P. macrostoma* (Foissner, 1982) as type-species and *P. terricola* (Buitkamp, 1977) as congener was established (Berger *et al.*, 1985). The diagnosis excludes, among others, taxa with a single left marginal cirral row. However, recently we found a very similar population with only 1 left marginal row. The morphogenesis of cell division was studied and compared with that of the type-species (Berger *et al.*, 1985) in order to decide whether or not the new population should be separated at the genus level.

MATERIAL AND METHODS

The population of hypotrichs was found on 2 May 1985 in the lower part of a bundle of straw which was in contact with the soil of a meadow in the city of Salzburg, Austria. The culture method and the protargol staining technique according to Foissner (1982) were used. All counts and measurements were performed at a magnification of 1000 × (1 unit = 1 µm).

The body shape of the living specimens was drawn from slides without cover slips. Details were studied on slightly to strongly squeezed individuals using an oil immersion objective (100 ×; eyepiece, 10 ×) and bright field illumination. Drawings of the impregnated specimens were made with a camera lucida. For clarity, parental cirri are shown in Figures 10–22 only by outline, whereas new ones are shaded.

The terminology is according to Kahl (1932), Borror (1972), and Corliss & Lom (1985).

RESULTS

Parakahliella haideri nov. spec.

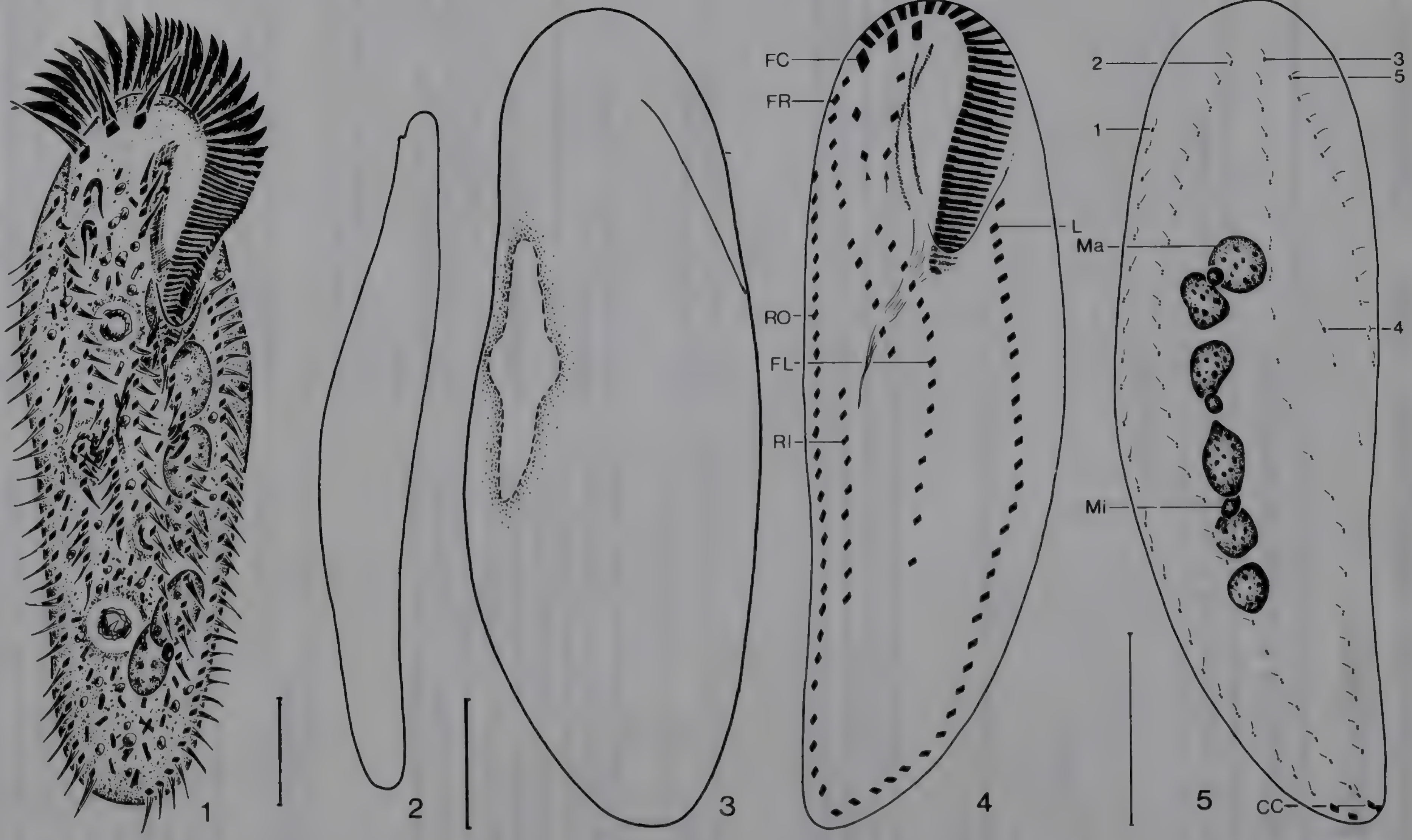
DIAGNOSIS. *In vivo* about 150 × 50 µm. 1 long and 1 short (sometimes absent) right and 1 left marginal row. 48 adoral membranelles and 6 macronuclear segments on average.

TYPE LOCATION. Frequent in a bundle of straw, which was in contact with the soil of a meadow in Salzburg, Austria.

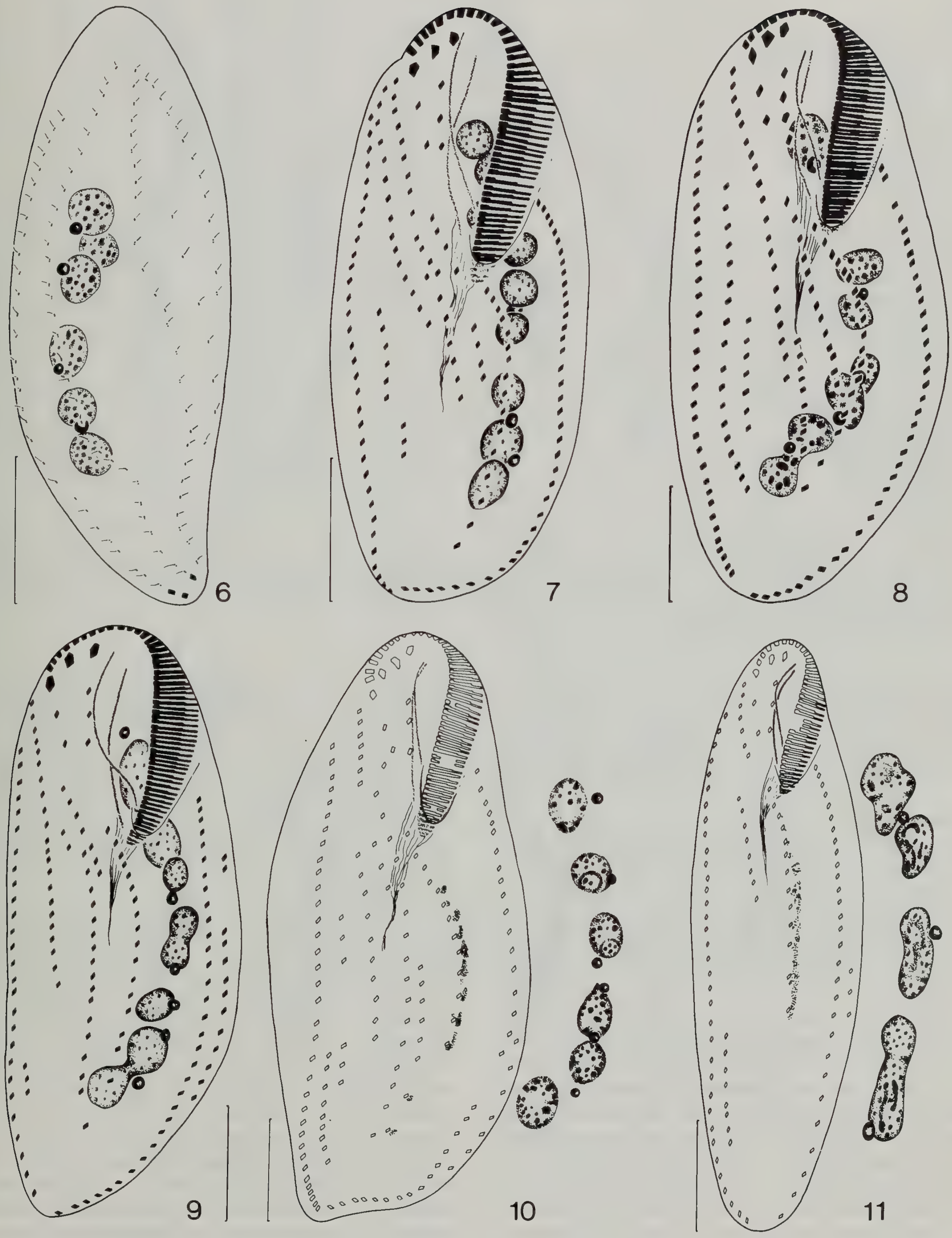
TYPE MATERIAL. A slide of holotype specimens and 1 slide of paratype specimens are deposited in the British Museum (Natural History): HOLOTYPE *N* 1987: 3: 19: 1; PARATYPE *N* 1987: 3: 19: 2.

DEDICATION. This species is named in honour of Dipl.-Ing. Reinhold Haider, director of the Hydrologische Untersuchungsstelle Salzburg, as a small token of appreciation of his continuous support of our work.

DESCRIPTION (Figs 1–9, Table 1). Body usually S-shaped, sometimes distinctly converging posteriad, very flexible but not contractile. Both ends rounded, about 2 : 1 flattened dorso-ventrally (Figs 1–3). Macronuclear segments ovoid, lying left of the median. Contractile vacuole on the left-hand border, above the middle of the cell, during diastole with



Figs 1–5 *Parakahliella haideri* from life (Figs 1–3) and after protargol impregnation (Figs 4, 5). **1–3**, ventral, lateral, and dorsal view. **4**, infraciliature in ventral view. Arrow, buccal row; arrow head, frontal row. **5**, infraciliature in dorsal view. Note the short kinety 4 of this specimen. Scale marks = 30 µm. CC, caudal cirri; FC, right frontal cirrus; FL, FR, left and right fronto-ventral row; L, left marginal row; Ma, macronuclear segment; Mi, micronucleus; RI,RO, inner and outer right marginal row; 1–5, dorsal kineties.



Figs 6–11 *Parakahliella haideri* after protargol impregnation. 6–9 Non-dividing specimens. 10, 11 Morphogenetical stages. **6**, dorsal view of a specimen with a dorsal kinety 4 of average length. **7**, **8**, ventral view of specimens with additional cirral rows. **9**, ventral view of a specimen with a second left marginal row. **10**, **11**, very early morphogenetic stages. Scale marks = 30 µm.

Table 1. Biometrical characterization of *Parakahliella haideri*[1]

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	127.1	125.5	12.5	1.978	9.8	105	160	40
Body, width	52.5	51.5	8.4	1.323	15.9	35	73	40
Adoral membranelles, No.	47.7	47.0	6.8	1.110	14.2	34	62	37
Adoral zone of membranelles, length	48.3	48.0	6.6	1.051	13.8	33	60	40
Macronuclear segments, No.	6.2	6.0	0.6	0.102	10.5	5	9	40
Posterior Ma, length	11.6	10.0	4.6	0.762	39.5	7	25	40
Posterior Ma, width	8.2	8.0	1.4	0.223	17.3	6	12	40
Micronuclei, No.	4.0	4.0	1.3	0.199	31.9	2	7	40
Posterior micronucleus, diameter	2.6	3.0	0.5	0.079	19.4	2	3	40
Enlarged frontal cirri, No.	3.0	3.0	0.4	0.063	13.2	2	5	39
Buccal row, No. cirri	3.0	3.0	0.7	0.104	22.2	1	4	40
Frontal row, No. cirri[2]	2.2	2.0	0.4	0.067	19.8	1	3	40
Left fronto-ventral row, No. cirri	13.6	13.0	3.4	0.563	25.2	4	20	37
Right fronto-ventral row, No. cirri	16.3	16.0	2.7	0.444	16.6	10	22	37
Left marginal row, No. cirri	32.3	32.0	3.9	0.613	12.0	23	40	40
Outer right marginal row, No. cirri	32.6	33.0	4.0	0.654	12.4	25	43	38
Inner right marginal row, No. cirri	9.3	8.0	4.7	0.798	50.9	2	18	35
Additional cirral rows, No.[3]	1.1	1.0	0.8	0.146	77.3	0	3	33
Dorsal kineties, No.	5.0	5.0	0	0	0	5	5	24
Dk 1, No. basal body pairs	28.5	28.0	3.5	0.653	12.4	21	34	29
Dk 2, No. basal body pairs	29.7	30.0	3.6	0.729	12.3	22	38	25
Dk 3, No. basal body pairs	26.4	27.0	3.4	0.686	12.7	19	33	24
Dk 4, No. basal body pairs	8.2	8.0	1.9	0.437	22.7	4	11	18
Dk 5, No. basal body pairs	12.1	12.0	1.9	0.359	15.4	9	16	27
Caudal cirri on Dk 1, No.	2.7	3.0	0.5	0.089	19.7	2	4	35
Caudal cirri on Dk 2, No.	1.1	1.0	0.3	0.056	29.3	1	2	34

[1] The data are based on protargol impregnated specimens. All measurements in µm. Legend: CV, coefficient of variation in %; Dk 1 – Dk 5; dorsal kinety 1–5, for the designation see Fig. 5; M, median; Ma, macronuclear segment; Max, maximum value; Min, minimum value; n, sample size; SD, standard deviation; SE, standard error of the arithmetic mean; x̄, arithmetic mean.

[2] The right enlarged frontal cirrus is not included.

[3] Single cirri and rows with only 2 or 3 cirri are not included.

short channels. Pellicle without subpellicular granules, cytoplasm colourless, filled with many yellow shining 2–4 µm large crystals and some food vacuoles with flagellates and ciliates (peritrichs, *Gonostomum* sp.). Movement moderately rapid gliding.

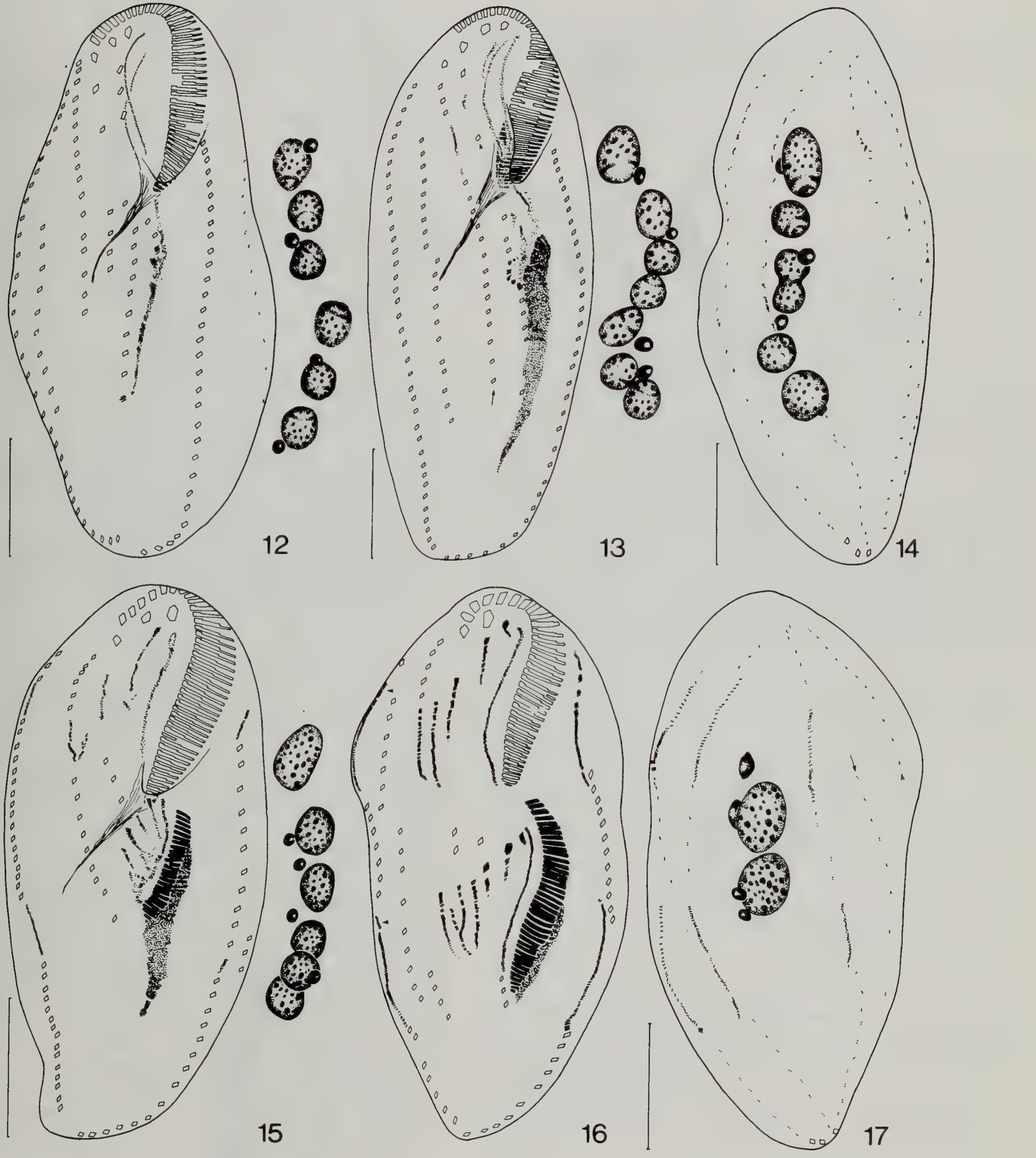
Adoral zone of membranelles usually formed like a question mark, about 40 % of body length, bases of the largest membranelles *in vivo* about 10 µm wide. Buccal area deep, undulating membranes slightly bent. Bases of the 3 frontal cirri distinctly enlarged. Cirri of the buccal row and the frontal row only slightly larger than the ventral and marginal cirri. Left fronto-ventral row usually in a line, but clearly separated from the short frontal row, begins anteriorly at about the level of the cytostome, terminates in the posterior half of the body. Right fronto-ventral row begins at the level of the right frontal cirrus, terminates usually in the middle of the cell. Rather frequent additional fronto-ventral rows occur, causing a great variability in the appearance of the ventral cirral pattern (Figs 7–9). Marginal rows inconspicuously separated posteriorly, cirri in vivo about 15 µm long. Very rarely (*c*. 1 of 50 specimens) a short second left marginal row occurs (Fig. 9). Dorsal cilia in vivo 2–3 µm long. Kinety 1 slightly shortened anteriorly, kineties 2 and 3 unshortened, kinety 4 shortened at both ends, and kinety 5 terminates in the middle of the cell. Dorsal rows 1 and 2 with caudal cirri.

MORPHOGENESIS OF CELL DIVISION (Figs 10–22). The earliest cortical morphogenetic event is the proliferation of basal bodies immediately left of the middle and posterior part of the left fronto-ventral row (Figs 10, 11). Subsequently a long and narrow oral primordium is formed (Fig. 12). The membranelles of the opisthe's adoral zone organize in a posterior direction. The buccal cirri, the second cirrus behind the right hypertrophied frontal cirrus, and some cirri in the anterior part of the right fronto-ventral row are modified to primordia. The parental undulating membranes commence with reorganization (Fig. 13). At about the same time the proliferation of new basal bodies occurs at 2 levels in the dorsal kineties 1, 2 and 3 (Fig. 14).

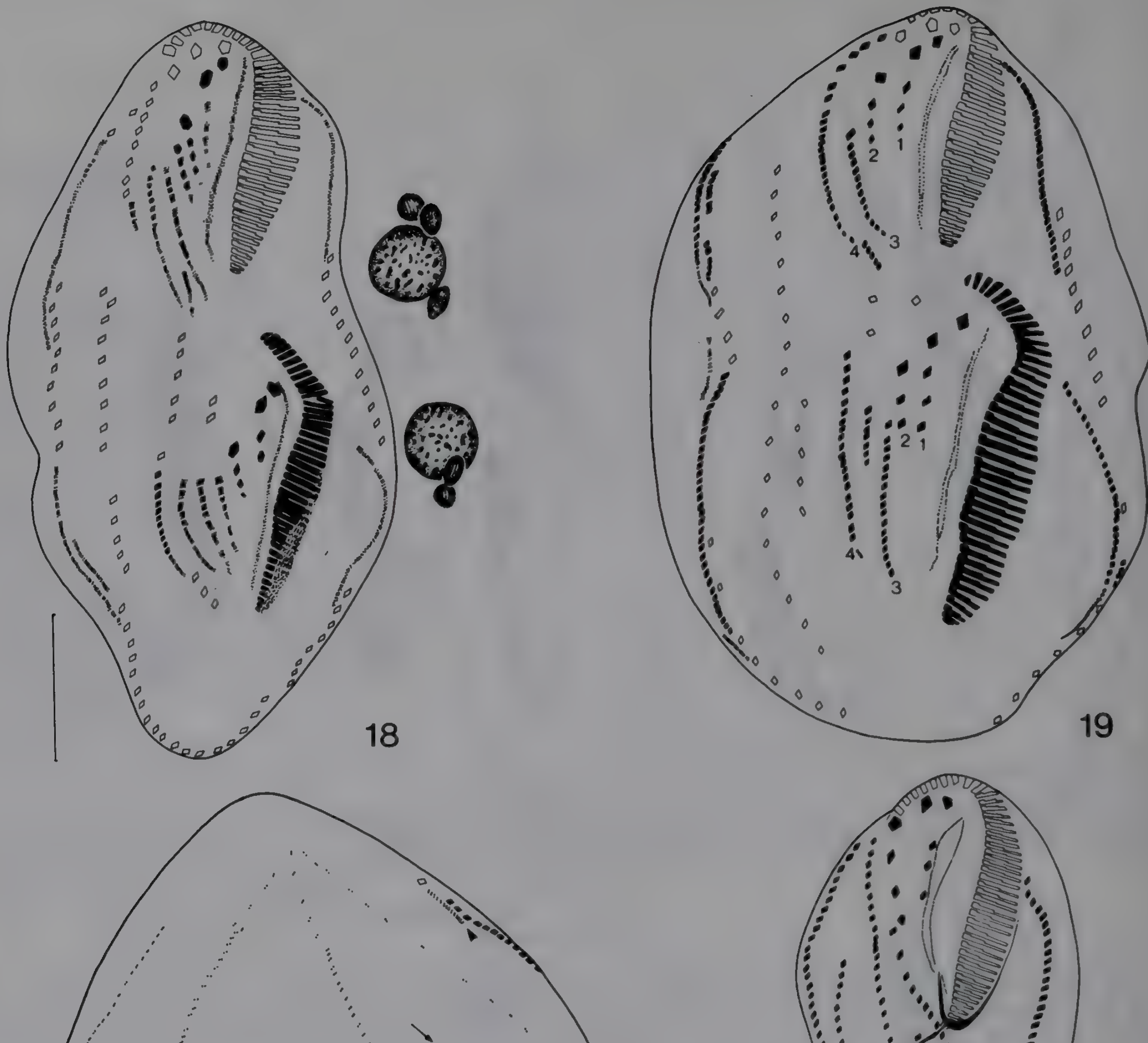
Division continues with the formation of the proter's and opisthe's marginal primordia and the further development of the fronto-ventral streaks. Usually 5 such streaks are formed, occasionally 6–9 occur (Fig. 15). Cortical morphogenesis proceeds with the cirral segregation from these streaks. At the anterior end of each right marginal primordium, 1 primordium of a dorsal kinety is separated and migrates onto the dorsal surface (Figs 16, 20). The primordia in the dorsal kineties 1–3 are elongated. The fusion of the macronuclear segments is almost completed (Fig. 17).

Figure 18 shows a late morphogenetic stage, where a large part of the opisthe's adoral zone is organized and the final number of membranelles recognizable. Many parental fronto-ventral and marginal cirri are still preserved. Parallel to the right marginal row of the opisthe there is a short marginal streak in this specimen which forms the inner right marginal row.

When the segregation of the fronto-ventral cirri is finished, the new left fronto-ventral rows become displaced in a posterior direction. At this stage the undulating membranes of both the proter and the opisthe are separated (Fig. 19).



Figs 12–17 Morphogenetical stages of *Parakahliella haideri* after protargol impregnation. **12**, early stage in ventral view. **13**, early stage in ventral view. Arrow, right fronto-ventral row; arrow head, frontal row. **14**, early stage in dorsal view. Arrow, parental dorsal kinety 4; arrow head, parental dorsal kinety 5. **15**, **16**, middle stages in ventral view. Arrow head, primordium of the new dorsal kinety 5. **17**, middle stage in dorsal view. Arrow, parental dorsal kinety 4; arrow head, parental dorsal kinety 5. Scale marks = 30 µm.



Figs 18–22 Morphogenetical stages of *Parakahliella haideri* after protargol impregnation. **18**, late stage in ventral view. **19**, very late stage in ventral view. 1, buccal row; 2, frontal row; 3, left frontoventral row; 4, right fronto-ventral row; arrow head, new dorsal kinety 5 of the opisthe. **20**, very late stage in dorsal view. Arrow, parental dorsal kinety 4; small arrow head, parental dorsal kinety 5; large arrow head, new dorsal kinety 5 of the proter. **21**, **22**, post divider in ventral and dorsal view. Scale marks = 30 µm.

The formation of the new dorsal kineties 1, 2 and 3 continues. Caudal cirri differentiate at the posterior end of the dorsal kineties 1 and 2. The parental kineties 4 and 5 are completely maintained. They form the new kinety 4 of the filial products (Figs 20, 22). After the separation of the proter and the opisthe the formation of the final cortical pattern is continued (Fig. 21).

DISCUSSION

SPECIES COMPARISON. *Parakahliella haideri* differs from both congeners in the possession of only 1 left marginal row. It can be further separated from *P. terricola* by the higher number of adoral membranelles (*P. haideri* $\bar{x}$ = 48, 34–62; *P. terricola* 28). All other biometrical and morphological characters overlap considerably (Buitkamp, 1977; Foissner, 1982; Berger *et al.*, 1985).

There is some evidence which suggests that there is a small variation in the number of the left marginal rows, even in species with normally only 1 row (Jeffries & Mellott, 1968; Grim, 1970; Walker & Grim, 1973; Borrow & Wicklow, 1983; Jerka-Dziadosz & Banaczyk, 1983). However, in many biometrical investigations this character was shown to be very stable in natural populations (e.g. Foissner, 1982, 1984; Berger *et al.*, 1985; Berger & Foissner, 1987; Wirnsberger *et al.*, 1985*a*, *b*). Thus, some variation might be caused by prolonged or suboptimal culture conditions and should not be included in species diagnosis.

Redefinition of the Genus *Parakahliella* Berger, Foissner & Adam, 1985

Parakahliella was originally characterized as 'Kahliellidae with caudal cirri and more than 1 right and 1 left marginal cirral row. Some parts of the parental left marginal infraciliature are preserved in the post-dividers' (Berger *et al.*, 1985). The species described in this paper agrees with the type-species *P. macrostoma* (Foissner, 1982) and *P. terricola* (Buitkamp, 1977) in the number and the arrangement of the fronto-ventral cirral rows and in particular with *P. macrostoma* in the formation of the fronto-ventral rows and the special morphogenetic pattern of the dorsal kineties. The conservation of the parental dorsal kineties 4 and 5 as new kinety 4 is a unique type of dorsal morphogenesis and a strong apomorphic character, which indicates the congenerity of the 3 species now included and separates *Parakahliella* from the other members of this family (Tuffrau, 1979; Foissner & Adam, 1983; Berger *et al.*, 1985). However, the diagnostic characters—'increased number of left marginal rows and preservation of some parts of the parental left marginal infraciliature'—would exclude *P. haideri* from this genus. Hence, we suggest a slight modification of the generic diagnosis of *Parakahliella*: Kahliellidae with caudal cirri and 1 or more right and left marginal rows. During morphogenesis some parental dorsal rows are conserved as new kinety in the filial products.

ACKNOWLEDGEMENTS. The photographical assistance of Mrs Karin Bernatzky is greatly acknowledged. The study was supported by the 'Fonds zur Förderung der wissenschaftlichen Forschung, Projekt Nr. P 5889'.

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Manuscript accepted for publication 16 March 1987

Bull. Br. Mus. nat. Hist. (Zool.) **55**(1): 19–46 Issued 25 May 1989

Morphology and biometry of some soil hypotrichs (Protozoa, Ciliophora) from Europe and Japan

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SYNOPSIS. The morphology and the infraciliature of 18 species of hypotrichous ciliates from various soils of Europe and Japan have been investigated by living observation and protargol staining. All species are characterized biometrically: *Holosticha islandica* nov. spec.; *H. sylvatica* Foissner, 1982; *Paruroleptus lepisma* Wenzel, 1953; *Birojimia terricola* nov. gen., nov. spec.; *Wallackia bujoreani* (Lepsi, 1951) nov. comb. (basionym: *Paraholosticha bujoreani* Lepsi, 1951); *Paraurostyla granulifera* nov. spec.; *Amphisiella polycirrata* nov. spec.; *A. quadrinucleata* nov. spec.; *Uroleptoides binucleata* Hemberger, 1985; *Hemisincirra inquieta* Hemberger, 1985; *H. vettersi* nov. spec.; *Terricirra matsusakai* nov. gen., nov. spec.; *Oxytricha islandica* nov. spec.; *O. lanceolata* Shibuya, 1930; *O. longigranulosa* nov. spec.; *Steinia muscorum* Kahl, 1932; *Urosoma octonucleata* nov. spec.; and *Euplotes corsica* nov. spec. Additionally, the ventral and dorsal infraciliature of the limnetic species *Laurentiella strenua* (Dingfelder, 1962) nov. comb. (basionym: *Paruroleptus strenuus* Dingfelder, 1962) is described. *Uroleptus muscorum* Kahl, 1932 is transferred to the new urostylid genus *Birojimia*: *B. muscorum* (Kahl, 1932) nov. comb. *Hemisincirra viridis* (Foissner, 1982) Foissner, 1984 and *H. livida* Berger & Foissner, 1987 are now included in the new oxytrichid genus *Terricirra*: *T. viridis* (Foissner, 1982) nov. comb. and *T. livida* (Berger & Foissner, 1987) nov. comb.

INTRODUCTION

Recently, we published the morphology of 18 species of hypotrichs from soils of Europe and Asia (Berger & Foissner, 1987). Some other new soil hypotrichs from these continents were described elsewhere (Foissner, 1986, 1987*a,b*; Berger & Foissner, 1988*a,b*). The present paper is concerned with the description of further hypotrichs from Austria, the Federal Republic of Germany, France, Iceland, Portugal, Spain and Japan.

MATERIALS AND METHODS

For the material see Table 1. The culture and staining methods were as given in Foissner (1979, 1982). The body shape of the living specimens was drawn from slides without cover slips. Details were studied on slightly to heavily squeezed individuals using an oil immersion objective (100 ×; eyepiece, 10 ×) and bright field illumination. Drawings of the protargol impregnated specimens were made with a camera lucida. One section of the scales in the drawings corresponds to 10μm. All counts and measurements were performed at a magnification of 1000 × (1 unit of the ocular micrometer = 1.4μm). The data in the Tables are based on protargol impregnated specimens. All measurements in μm. The statistical procedures are described in Sokal & Rohlf (1981). The following sample statistics were calculated: x̄, arithmetic mean; M, median; SD, standard deviation; SE, standard error of the arithmetic mean; CV, coefficient of variation in %; Min, Max, minimum and maximum value; n, sample size.

The terminology is according to Kahl (1932), Borror (1972), Curds (1975), and Corliss & Lom (1985).

One slide of holotype specimens and 1 slide of paratype specimens of the new species and 1 neotype-slide of each other species described have been deposited in the British Museum (Natural History) in London. The reference numbers of the slides are shown in Table 1.

DESCRIPTIONS OF SPECIES

Holosticha islandica nov. spec.

Diagnosis. *In vivo* about 80–100 × 25 μm, long ellipsoid. Subpellicular granules yellowish, spherical (< 0.5 μm). Usually 6–7 midventral pairs and 3–4 transverse cirri. 17 adoral membranelles and 16 macronuclear segments on average. 3 dorsal kineties.

Table 1. Localities of the populations and reference numbers of the type-slides (protargol silver impregnated) deposited in the British Museum (Natural History) in London

Species (Reference numbers)	Date	Locality
Amphisiella polycirrata 1988 : 2 : 1 : 1, holotype 1988 : 2 : 1 : 2, paratype	July 1985	Slightly redish-brown soil grown with *Opuntia ficus-indica* and tufts of grass (0 – 5 cm). pH = 4.8. Sea-level: *c.* 150 m. Garajan Kap, Madeira,Portugal.
Amphisiella quadrinucleata 1988 : 2: 1: 3 holotype 1988 : 2 :1: 4 paratype	20.3.1985	Yellowish soil with poorly decomposed needles. pH = 3.8. Sea-level: 10 – 20 m. Mea-Shima, Amakusa, Kumamoto Prefecture, Japan.
Birojimia terricola 1988 : 2: 1 : 5 holotype 1988 : 2: 1 : 6 paratype	6.4.1985	Brown soil of a deciduous forest with many fragments of leaves and roots. pH = 3.8. Sea-level: 5 – 10 m. Biro-Jima, Amakusa, Kumamoto Prefecture, Japan.
Euplotes corsica 1988 : 2 : 1: 7 hapantotype 1988 : 2 : 1 : 8 hapantotype 1988 : 2 : 1 : 9 parahapantotype	Summer 1985	Fine, grey soil of a saline pool on the base of a vineyard at Etang d'Urbino, Corsica, France.
Hemisincirra inquieta 1988 : 2 : 1: 10	8.8.1985	Litter and dark (volcanic) upper soil layer of a heath with dwarf shrubs (dominated by *Betula nana, Empetrum nigrum, Vaccinium uliginósum, Arctostáphylos úva-úrsi*). pH = 5.5. Sea-level: 120 m. Gooa Foss, Bardårdalur, North-Iceland.
Hemisincirra vettersi 1988 : 2 : 1 :11 holotype 1988 : 2 : 1 : 12 paratype	9.8.1985	Soil with tufts of *Alchemilla alpina* of a postglacial basalt desert. pH = 6.2. Sea-level: 340 m. Dettifoss, Neisland, Sökullsá a Fjellum, Iceland.
Holosticha islandica 1988 : 2 : 1 : 13 paratype	8.8.1985	See *Hemisincirra inquieta*.
Holosticha sylvatica 1988 : 2 : 1 : 14	20.3.1985	See *Amphisiella quadrinucleata*.
Laurentiella strenua		A protargol slide of this fresh-water species was kindly supplied by Dr J. Martin, Spain.
Oxytricha islandica 1988 : 2 : 1 : 15 holotype 1988 : 2 : 1 : 16 paratype	7.8.1985	Soil of a pasture with *Deschámpsia caespitósa* and moss, about 100 m far from the beach. pH = 5.8. Sea-level: 30 m. Peninsula Vatnsney 'Hvitserkur', Iceland.
Oxytricha lanceolata 1988 : 2 : 1 : 17	July 1985	Redish soil of a heath with grass. Sea-level: *c.* 1800 m. Pico de Arieiro, Madeira, Portugal.
Oxytricha longigranulosa 1988 : 2 : 1 : 18 holotype 1988 : 2 : 1 : 19 paratype	6.4.1985	Brown soil of a deciduous forest with many fragments of leaves and roots. pH = 3.5. Sea-level: 682 m. Mt. Kura-Take, Amakusa, Kumamoto Prefecture, Japan.
Paraurostyla granulifera 1988 : 2 : 1 : 20 holotype 1988 : 2 : 1 : 21 paratype	6.4.1985	Brown soil of a deciduous forest with many fragments of leaves and roots. pH = 4.8. Sea-level: 470 m. Mt. Ryu-Ga-Take, Amakusa, Kumamoto Prefecture, Japan.
Paruroleptus lepisma	July 1985	See *Amphisiella polycirrata*.
1988 : 2 : 1 : 22	29.10.1982	Upper soil layer (0 – 5 cm) of a salt-steppe in the so-called 'Hölle' in Seewinkel. Mull at the edge of a small salt lake about 100 m north-east of the Oberen Stinkersee. Sea-level: 115 m. Burgenland, Austria.
Steinia muscorum 1988 : 2 : 1 : 23	Autumn 1985	Litter (0 – 3 cm) of a beechforest. Bergheim, Salzburg, Austria.
Terricirra matsusakai 1988 : 4 : 10 : 1 holotype 1988 : 4 : 10 : 2 paratype	25.3.1985	Soil of a rice field of Kyokushi. pH = 4.5. Kumamoto Prefecture, Japan.
Uroleptoides binucleata 1988 : 2 : 1 : 24 1988 : 2 : 1 : 25	7.8.1986	Litter and upper soil layer of a deciduous forest with *Pinus sylvéstris*. pH = 4.2. Berlin, FRG.
Urosoma octonucleata 1988 : 2 : 1 : 26 holotype 1988 : 2 : 1 : 27 paratype	July 1985	See *Amphisiella polycirrata*.
Wallackia bujoreani 1988 : 2 : 1 : 28 neotype	Summer 1985	Sandy brown soil with litter of grass, 10 m away from a small river. pH = 4.1. Sea-level: 500 – 600 m. Near the reservoir Ajaccio, Corsica, France.

TYPE LOCATION. Soil of a heath with dwarf shrubs, Gooa Foss, Bardårdalur, North-Iceland.

DESCRIPTION (Figs 1–4, Tables 1, 2). Left and right body margin straight, both ends rounded. About 2:1 flattened. Macronuclear segments *in vivo* 6–8 × 3–4 µm, most of them lying distinctly left of the median, 2–3 pieces are always situated right of the median at about the level of the cytostome. Contractile vacuole in about the middle of the cell, during diastole with inconspicuous channels. Subpellicular granules irregularly and loosely arranged. Cytoplasm colourless, with some 1–4 µm large, yellowish fat globules and 5–8 µm large food vacuoles with bacteria and fungal spores.

Adoral zone of membranelles about 28% of body length, bases of the largest membranelles *in vivo c.* 5 µm wide. Buccal area flat and narrow. Bases of the frontal cirri only slightly enlarged. Midventral rows terminate in about the middle of the cell. Marginal rows distinctly separated

Table 2. Biometrical characterization of *Holosticha islandica* (upper line) and *Holosticha sylvatica* (lower line)

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	74.5	75.0	6.0	1.670	8.1	66.0	86.0	13
	127.0	126.0	9.0	2.724	7.1	112.0	140.0	11
Body, width	20.5	21.0	2.7	0.739	13.0	16.0	25.0	13
	52.0	49.0	8.3	2.512	16.0	43.0	70.0	11
Adoral membranelles, number	17.5	17.0	0.8	0.215	4.4	16.0	19.0	13
	44.1	44.0	3.7	1.099	8.3	39.0	49.0	11
Adoral zone of membranelles, length	20.6	21.0	0.7	0.180	3.2	19.0	21.0	13
	44.5	43.0	2.9	0.888	6.6	40.0	49.0	11
Macronuclear segments, number	16.0	16.0	0.8	0.226	5.1	14.0	17.0	13
	56.0	56.0	4.1	1.228	7.3	50.0	61.0	11
Posterior macronuclear segment, length	5.6	6.0	1.1	0.311	20.0	4.0	7.0	13
	6.1	7.0	1.5	0.436	23.7	4.0	8.0	11
Posterior macronuclear segment, width	3.2	3.0	0.6	0.166	18.5	3.0	5.0	13
	4.1	4.0	0.7	0.211	17.1	3.0	5.0	11
Micronuclei, number	2.2	2.0	1.6	0.451	75.5	1.0	7.0	13
	2.2	2.0	0.4	0.122	18.5	2.0	3.0	11
Posterior micronucleus, length	1.6	1.6	0.1	0.037	8.5	1.4	1.8	13
	3.0	3.0	0	0	0	3.0	3.0	11
Posterior micronucleus, width	1.5	1.5	0.1	0.021	5.1	1.4	1.6	13
	3.0	3.0	0	0	0	3.0	3.0	11
Left marginal row, number of cirri	17.9	18.0	1.6	0.436	8.8	14.0	20.0	13
	37.2	39.0	4.3	1.292	11.5	31.0	43.0	11
Right maringal row, number of cirri	17.9	18.0	1.9	0.532	10.8	15.0	21.0	13
	40.9	42.0	4.7	1.417	11.5	30.0	47.0	11
Left midventral row, number of cirri[1]	5.5	6.0	0.5	0.144	9.4	5.0	6.0	13
	16.7	16.5	1.5	0.444	8.8	14.5	19.5	11
Right midventral row, number of cirri	6.7	7.0	1.0	0.263	14.2	5.0	8.0	13
	–	–	–	–	–	–	–	0
Frontal cirri, number[2]	3.0	3.0	0	0	0	3.0	3.0	13
	7.0	7.0	0	0	0	7.0	7.0	11
Buccal cirri, number	1.0	1.0	0	0	0	1.0	1.0	13
	1.0	1.0	0	0	0	1.0	1.0	11
Frontoterminal cirri, number	2.0	2.0	0	0	0	2.0	2.0	13
	2.0	2.0	0	0	0	2.0	2.0	11
Ventral cirri near the transverse cirri, number	–	–	–	–	–	–	–	0
	2.0	2.0	0	0	0	2.0	2.0	11
Transverse cirri, number	3.6	4.0	0.7	0.180	18.0	2.0	4.0	13
	8.3	8.0	1.1	0.333	13.3	6.0	10.0	11
Caudal cirri, number	1.5	2.0	0.7	0.183	42.9	0	2.0	13
	4.0	4.0	0.6	0.191	15.8	3.0	5.0	11
Dorsal kineties, number	3.0	3.0	0	0	0	3.0	3.0	13
	5.0	5.0	0	0	0	5.0	5.0	11
Distance 1[3]	–	–	–	–	–	–	–	0
	88.9	88.0	5.3	1.609	6.0	81.0	98.0	11

[1] For *H. sylvatica* the number of midventral pairs is listed

[2] In *H. sylvatica* the cirri behind the left frontal cirrus are included.

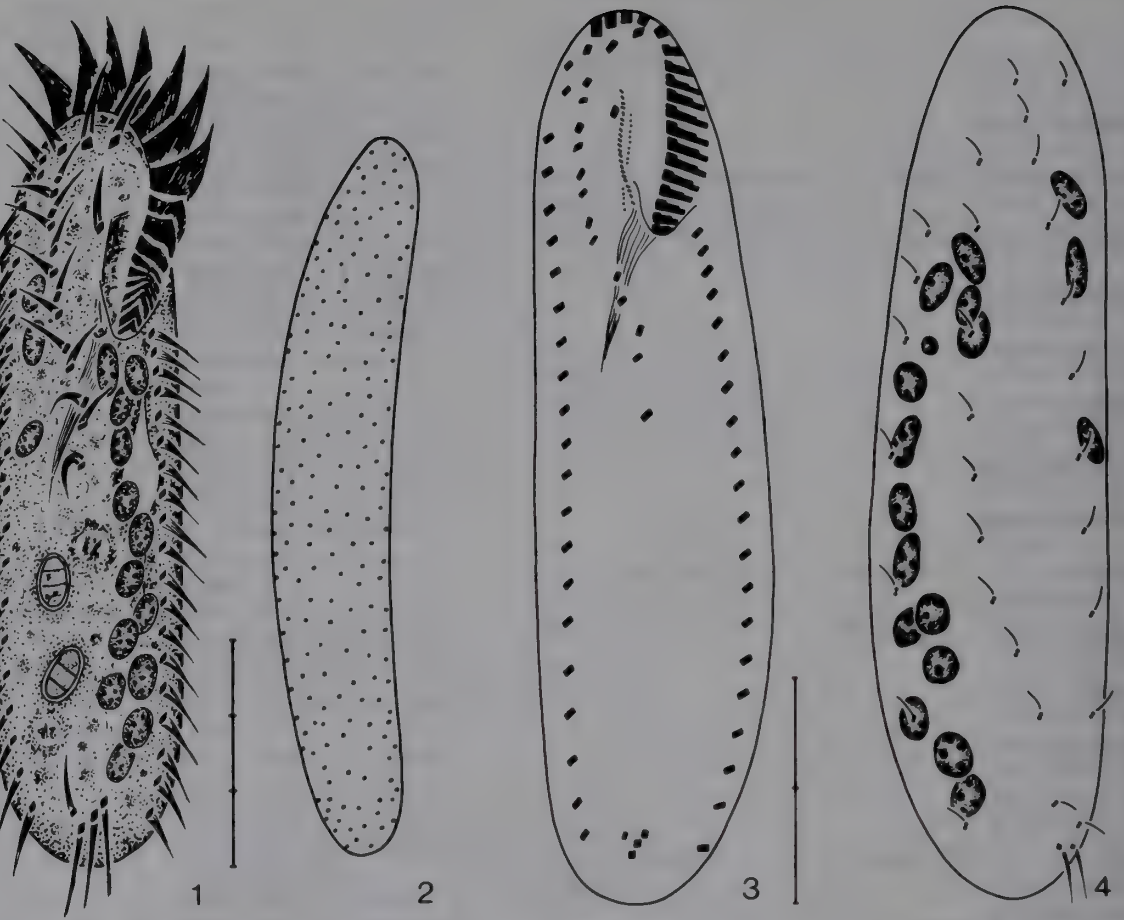
[3] Distance 1, distance between the anterior end of the cell and the posterior end of the midventral rows.

posteriorly, cirri *in vivo c.* 10 µm long. Usually a small cirrus (ventral cirrus ?) near the *in vivo* about 14 µm long transverse cirri. Dorsal kineties 1 and 2 slightly shortened anteriorly, kineties 2 and 3 usually with a small caudal cirrus each. Left of the anterior end of kinety 3 constantly a single basal body pair. Dorsal cilia *in vivo c.* 3 µm long.

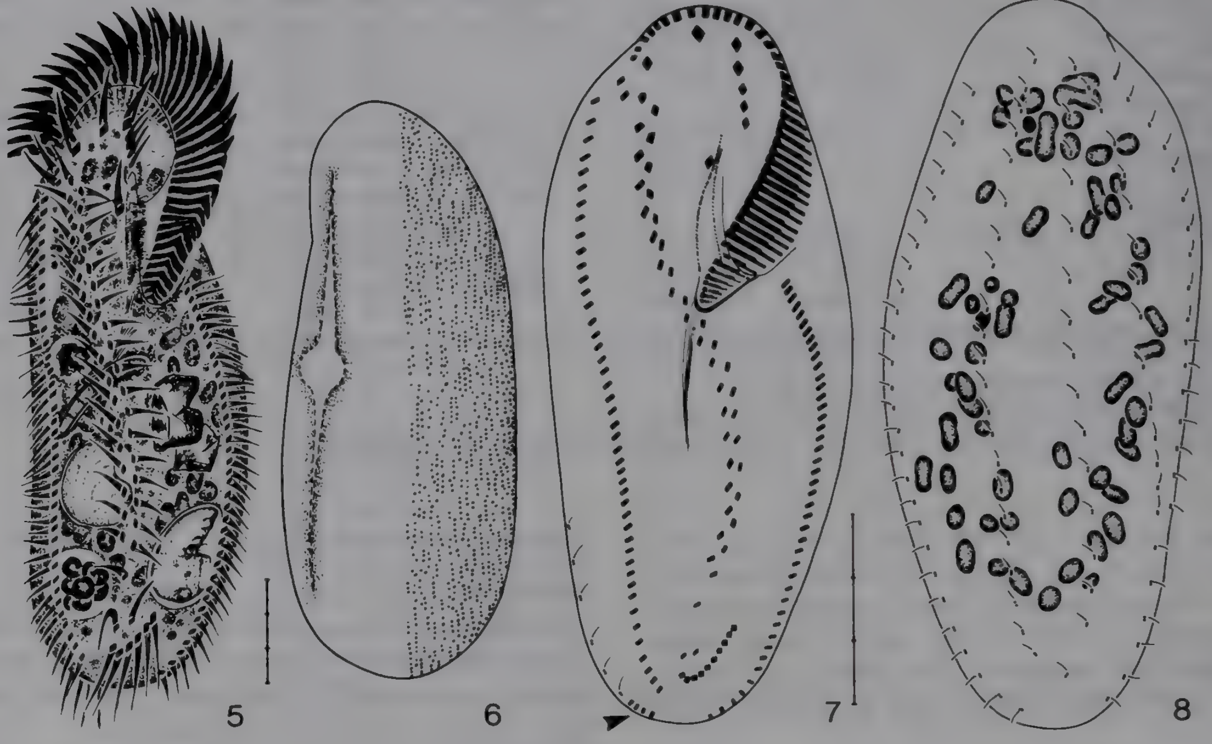
COMPARISON WITH RELATED SPECIES. *Holosticha islandica* resembles *H. tetracirrata* Buitkamp & Wilbert, 1974, which has 2 inconspicuous caudal cirri too (Foissner, 1982). However, it differs in some important biometrical characters *viz.* number of adoral membranelles, dorsal kineties, macronuclear segments, midventral pairs and by the possession of subpellicular granules from *H. tetracirrata*.

Holosticha sylvatica Foissner, 1982

DISCUSSION AND ADDITIONAL OBSERVATIONS (Figs 5–8, Tables 1, 2). Although the population from Japan is of the same size as the type material (Foissner, 1982) it has a distinctly higher number of macronuclear segments (Japanese population x̄ = 56, extremes = 50–61; type material 32, 28–36), adoral membranelles (44, 39–49; 35, 33–38), right (42, 30–47; 32, 28–40) and left marginal cirri (37, 31–43; 31, 25–35), pairs of midventral cirri (17, 14.5–19.5; 13, 10–15), cirri behind the left frontal cirrus (4; 1–2), and caudal cirri (4, 3–5; 2). Borror & Wicklow (1983) observed 2–5 cirri behind the left frontal cirrus and 12–19 pairs of midventral cirri in 5 populations of this species. Because of the obviously high intraspecific variability of these characters we give a complete biometrical



Figs 1–4 *Holosticha islandica* from life (Figs 1, 2) and after protargol impregnation (Figs 3, 4). **1, 2** Ventral and lateral view. Figure 2 shows the arrangement of the yellowish subpellicular granules. **3, 4** Infraciliature in ventral and dorsal view.



Figs 5–8 *Holosticha sylvatica* from life (Figs 5, 6) and after protargol impregnation (Figs 7, 8). **5, 6** Ventral and dorsal view. The right side of Figure 6 shows the arrangement of the colourless subpellicular granules. **7, 8** Infraciliature in ventral and dorsal view. Arrow head, caudal cirri.

Table 3 Biometrical characterization of *Paruroleptus lepisma*

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	132.6	130.0	8.1	2.238	6.1	120.0	147.0	13
Body, width	38.9	39.0	3.5	0.964	8.9	34.0	46.0	13
Adoral membranelles, number	33.0	33.0	1.9	0.519	5.7	29.0	36.0	13
Adoral zone of membranelles, length	36.2	36.0	2.5	0.699	7.0	31.0	41.0	13
Macronuclear segments, number	2.0	2.0	0	0	0	2.0	2.0	13
Posterior macronuclear segment, length	17.5	18.0	2.4	0.676	14.0	13.0	21.0	13
Posterior macronuclear segment, width	8.2	8.0	0.9	0.249	11.0	7.0	10.0	13
Distance between the macronuclear segments	2.7	3.0	2.0	0.548	73.3	0	7.0	13
Micronuclei, number	2.3	2.0	0.6	0.175	27.3	1.0	3.0	13
Posterior micronucleus, length	4.0	4.0	0.5	0.127	11.4	3.0	5.0	13
Posterior micronucleus, width	2.9	3.0	0.3	0.087	11.1	2.0	3.0	13
Left marginal row, number of cirri	28.8	28.0	1.8	0.496	6.2	26.0	32.0	13
Right marginal row, number of cirri	27.5	28.0	1.9	0.526	6.9	24.0	30.0	13
Left midventral row, number of cirri	18.9	19.0	1.9	0.512	9.8	15.0	22.0	13
Right midventral row, number of cirri	19.5	19.0	1.8	0.501	9.3	16.0	23.0	13
Distance 1[1]	109.9	110.0	7.5	2.066	6.8	98.0	122.0	13
Frontal cirri, number[2]	4.0	4.0	0	0	0	4.0	4.0	13
Buccal cirri, number	1.0	1.0	0	0	0	1.0	1.0	13
Frontoterminal cirri, number	3.0	3.0	0	0	0	3.0	3.0	13
Ventral cirri near the transverse cirri, number	1.0	1.0	0	0	0	1.0	1.0	13
Transverse cirri, number	4.0	4.0	0	0	0	4.0	4.0	13
Distance 2[3]	8.4	8.0	1.8	0.500	21.5	7.0	13.0	13
Caudal cirri, number	3.0	3.0	0	0	0	3.0	3.0	13
Dorsal kineties, number	5.0	5.0	0	0	0	5.0	5.0	13

[1] Distance 1, distance between the anterior end of the cell and the posterior end of the midventral rows.
[2] The cirrus behind the right frontal cirrus is included.
[3] Distance 2, distance between the posterior transverse cirrus and the posterior end of the cell.

characterization of the Japanese population and describe some additional and deviating observations.

Close beneath the pellicle there are very many, less than 0.5 μm diameter colourless subpellicular granules, arranged in short longitudinal rows. Cytoplasm filled with 2–5 μm large, fat globules, many food vacuoles containing globular cyanobacteria, fungal spores, and ciliates (*Colpoda inflata*), and some pieces of quartz. There is always an accumulation of fat globules in the frontal area. Cytoproct left, near the posterior end of the cell. Movement rapid.

Bases of the largest adoral membranelles *in vivo c.* 8 μm wide. Left marginal row terminates at the posterior end of the cell, marginal cirri about 13 μm long. Midventral rows terminate shortly before the transverse cirri. Caudal cirri exist at the posterior end of the dorsal kinety 5 only, a feature which is recognizable from the original description too (Foissner, 1982). This unusual position is also described in *Keronella gracilis* Wiackowski, 1985.

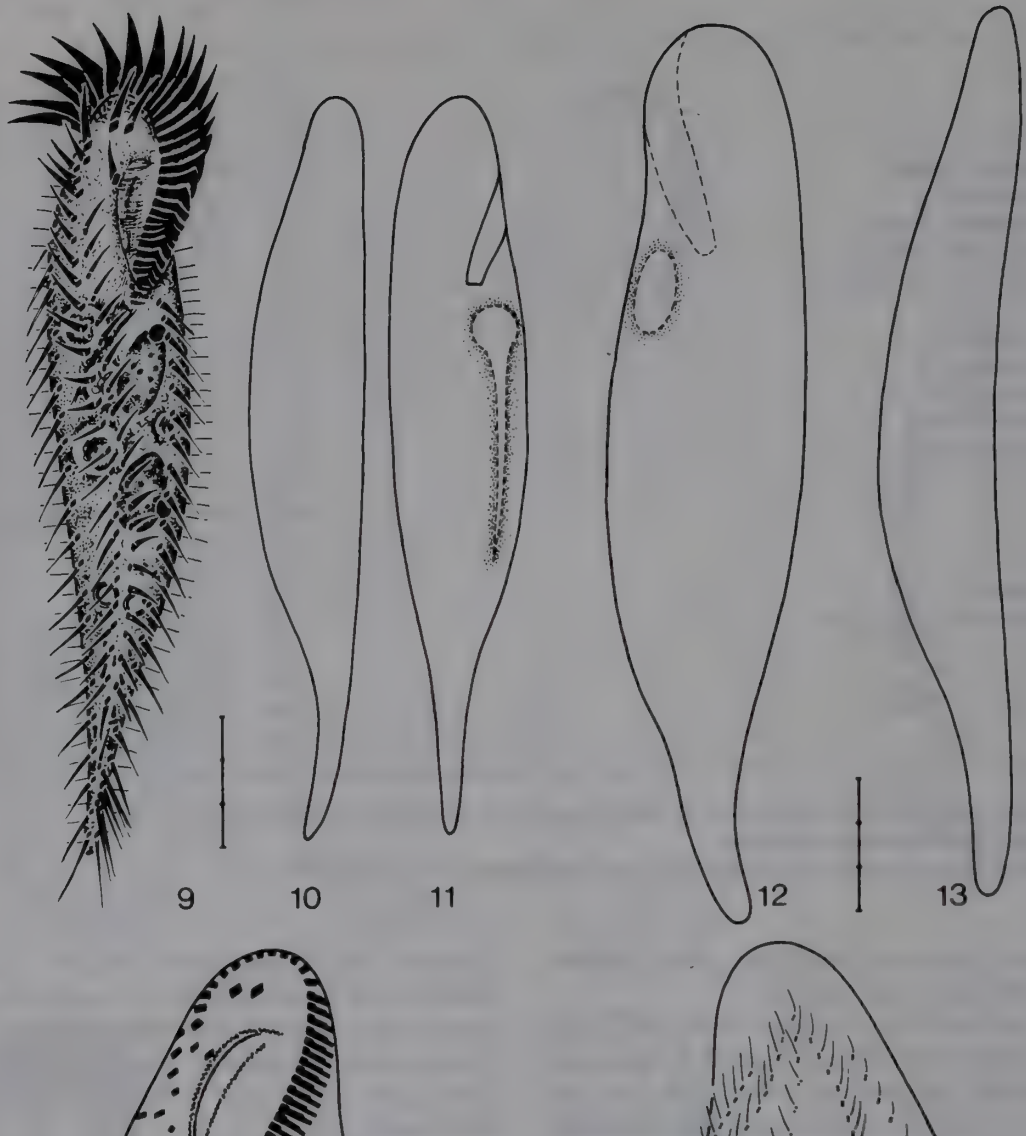
Paruroleptus lepisma Wenzel, 1953

Redescription (Figs 9–15, Tables 1, 3). The infraciliatures of the 2 populations studied are identical. Thus, from the population of Burgenland only the *in vivo* aspect of the body shape and some deviating and additional characters are described.

In vivo 160–200 × 45–55 μm, slender, anterior end rounded, conspicuously tapered posteriorly. Slightly (10–20%) contractile, very flexible. Not or slightly flattened dorso-ventrally. Macronuclear segments *in vivo c.* 22–25 × 11–14 μm, lying slightly left of the median of the cell. Micronuclei spherical (4 μm, Madeira) or ellipsoid (8 × 5 μm, Burgenland). Contractile vacuole close behind the adoral zone of membranelles, during diastole with a posterior channel. Subpellicular granules absent. Cytoplasm colourless, especially in the posterior part with many crystals. Food vacuoles 5–15 μm, with bacteria, fungal spores, flagellates, cysts of naked amoebae, testaceans (*Euglypha* sp.), and ciliates. Slow to moderately fast movement.

Adoral zone of membranelles *c.* 27% of body length, bases of the largest membranelles *in vivo* 7–8 μm wide. Buccal area deep, undulating membranes long, distinctly bent in the protargol slides. 3 frontal cirri and buccal cirrus slightly enlarged. Bases of the left cirri of the midventral pairs distinctly smaller than those of all other cirri. Midventral rows almost extend to posterior. Distance between the marginal cirri increases in the posterior direction. Marginal cirri *in vivo c.* 20 μm long. Transverse cirri inconspicuous, *in vivo c.* 22 μm long. Dorsal kineties 1–3 not shortened, with caudal cirri at the posterior tip of the cell, rows 4 and 5 slightly shortened anteriorly. The middle part of kinety 1 extends onto the ventral surface. Dorsal cilia motile, *in vivo* about 5–7 μm long.

Discussion. The identification of our population as *P. lepisma* is based on correspondence with the body shape, the ventral infraciliature, the number of dorsal kineties and length of the cilia, and the terrestrial habitat. Differences exist in the body size (type population 90–100 μm; our population 160–200 μm) and the movement (rapid; slow to moderately fast). It can be distinguished from the congeneric species by the body size, the number of transverse cirri, dorsal kineties, and macronuclear segments, and the habitat (Kowalewski, 1882; Stokes, 1886; Kahl, 1932; Horváth, 1933; Wang & Nie, 1935; Gelei, 1954; Reuter, 1961; Vuxanovici, 1963; Grolière, 1975; Foissner, 1980, 1982, 1984; Berger & Foissner, 1987).



Figs 9–15 *Paruroleptus lepisma* from life (Figs 9–13) and after protargol impregation (Figs 14, 15). **9–11** Ventral and lateral views of the population from Madeira. **12, 13** Dorsal and lateral view of the population from Burgenland. **14, 15** Infraciliature in ventral and dorsal view of the population from Madeira.

Table 4 Biometrical characterization of *Birojimia terricola*

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	180.1	186.0	26.7	7.577	14.6	126.0	215.0	12
Body, width	37.2	36.5	3.8	1.107	10.3	32.0	43.0	12
Adoral membranelles, number	39.1	40.0	3.1	0.883	7.8	35.0	43.0	12
Adoral zone of membranelles, length	54.6	55.0	5.2	1.495	9.5	46.0	63.0	12
Macronuclear segments, number	60.7	61.0	3.5	0.995	5.7	55.0	65.0	12
Posterior macronuclear segment, length	5.6	6.0	1.2	0.358	22.2	4.0	7.0	12
Posterior macronuclear segment, width	4.1	4.0	0.8	0.229	19.4	3.0	5.0	12
Posterior micronucleus, length	3.5	3.5	0.6	0.224	15.6	3.0	4.0	6
Posterior micronucleus, width	2.7	3.0	0.5	0.211	19.4	2.0	3.0	6
Left marginal row, number of cirri	47.3	48.0	4.7	1.345	9.8	40.0	53.0	12
Right marginal row 1, number of	41.2	40.5	5.5	1.590	13.4	32.0	49.0	12
cirri/distance[1]	14.6	15.0	2.5	0.733	17.4	8.0	18.0	12
Right marinal row 2, number of	28.9	29.0	5.0	1.433	17.2	22.0	38.0	12
cirri/distance[1]	44.3	43.5	11.6	3.354	26.2	29.0	63.0	12
Right marginal row 3, number of	19.1	20.0	4.7	1.357	24.6	13.0	27.0	12
cirri/distance[1]	70.3	75.0	13.9	4.023	19.8	35.0	88.0	12
Right marginal row 4, number of	6.9	7.0	3.4	0.973	48.7	3.0	13.0	12
cirri/distance[1]	135.4	139.0	27.6	7.955	20.3	92.0	200.0	12
Midventral pairs, number/distance[2]	13.2	13.0	2.2	0.619	16.3	10.5	16.5	12
	107.2	106.0	18.3	5.291	17.1	75.0	133.0	12
Enlarged frontal cirri, number	3.0	3.0	0	0	0	3.0	3.0	12
Buccal cirri, number	1.0	1.0	0	0	0	1.0	1.0	12
Frontoterminal cirri, number	1.8	2.0	0.7	0.207	39.1	0	3.0	12
Ventral cirri near the transverse cirri, number	1.8	2.0	0.5	0.131	25.8	1.0	2.0	12
Transverse cirri, number	5.2	5.0	0.8	0.241	16.2	4.0	6.0	12
Caudal cirri, number	3.6	3.0	1.6	0.466	44.0	2.0	7.0	12

[1] For the designation of the right marinal rows see Figure 17. Upper line, number of cirri; lower line, distance between the anterior end of the cell and the anterior cirrus.

[2] Upper line, number of midventral pairs; lower line, distance between the anterior end of the cell and the posterior end of the midventral rows.

BIROJIMIA nov. gen.

DIAGNOSIS. Slender, posteriorly converging Urostylidae with 1 left and 2 or more right marginal rows. 3 slightly to distinctly enlarged frontal cirri. Transverse and caudal cirri present.

TYPE-SPECIES. *Birojimia terricola* nov. spec.

COMPARISON WITH RELATED GENERA. *Birojimia* differs from *Uroleptus* Ehrenberg, 1832a, and *Paruroleptus* Kahl, 1932 by having more than 1 right marginal row. It can be distinguished from *Urostyla* Ehrenberg, 1832*b* by the slender, posteriorly converging body shape, the lower number of frontal cirri, and especially by its single left marginal row (Kahl, 1932; Borror & Wicklow, 1983).

The second species which has to be included in the new genus is *Uroleptus muscorum* Kahl, 1932: *Birojimia muscorum* (Kahl, 1932) nov. comb. This is evident from the redescription of Foissner (1982), who combined it with *Paruroleptus*.

The successive reduction of the number of cirri in the right marginal rows of *B. terricola* strongly supports the idea of Borror (1979) and Berger *et al.* (1985) that marginal rows and dorsal kineties are very probably homonomous structures.

Birojimia terricola nov. spec.

DIAGNOSIS. *In vivo* about 155 × 40 μm. Midventral rows terminate roughly in the middle of the cell. About 6 right marginal rows, successively shortened anteriorly from left to right. 39 adoral membranelles, 5 transverse cirri, and 61 macronuclear segments on average.

TYPE LOCATION. Soil in Biro-Jima, Amakusa, Kumamoto Prefecture, Japan.

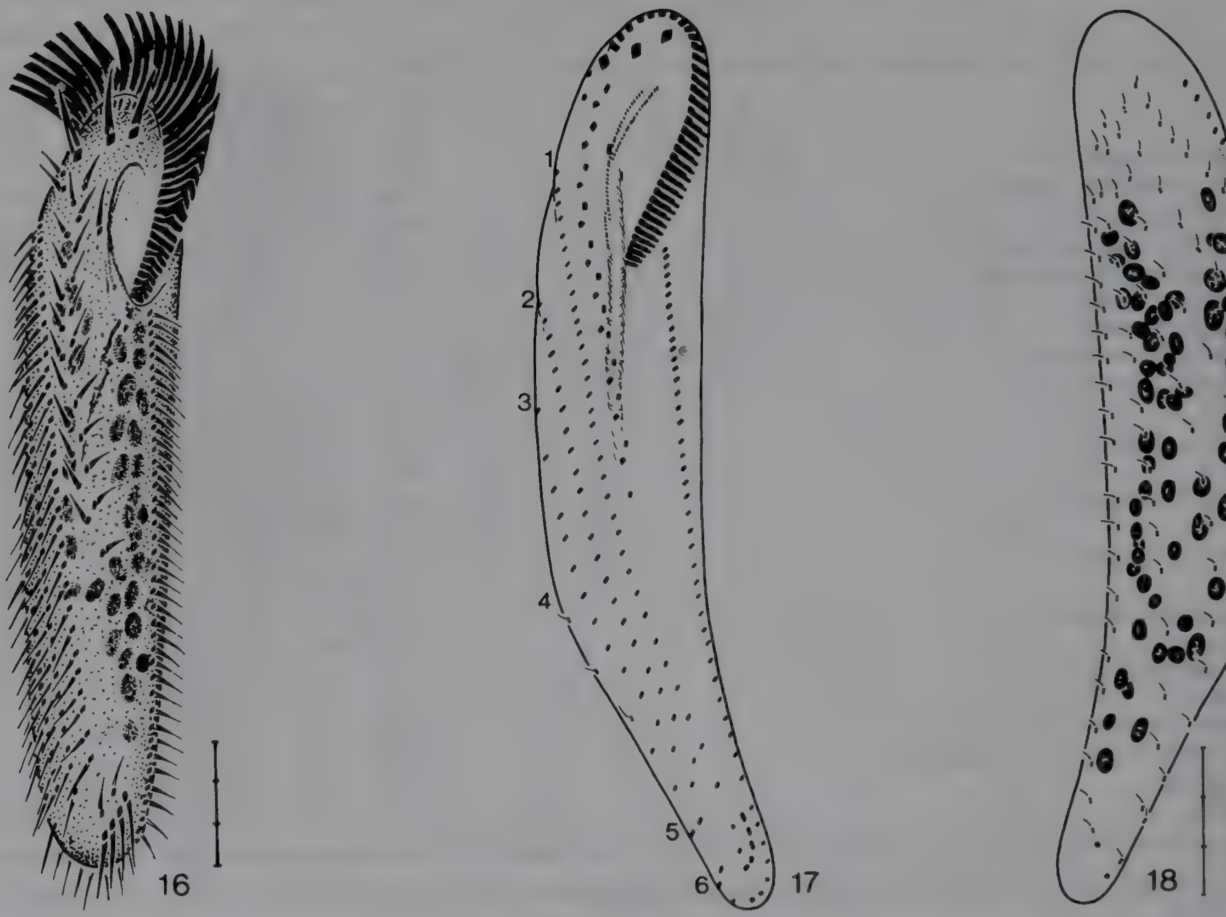
DESCRIPTION (Figs 16–18, Tables 1, 4). Body slender, slightly twisted and converging posteriad. Both ends rounded. Macronuclear segments *in vivo* 6–7 × 4–5 μm, micronuclei *in vivo c.* 6 × 4 μm, do not impregnate with protargol. Subpellicular granules absent, cytoplasm colourless. Feeds on fungi, flagellates, and ciliates (*Vorticella astyliformis, Colpoda fastigata*).

Adoral zone of membranelles *c.* 30% of body length, buccal area deep. Undulating membranes long, slightly bent. Buccal cirrus inserted roughly in the middle of the paroral membrane. Pharyngeal fibres conspicuous after protargol impregnation. Bases of the frontal cirri distinctly enlarged. Inner right marginal row (row 1) not shortened, extends onto the dorso-lateral surface anteriorly. Rows 2–6 consist of cirri and basal body pairs with typical dorsal cilia. Rows 5 and 6 consist of 2–3 cirri only. Bases of the transverse cirri scarcely enlarged. Dorsal kinety 1 usually with 2 caudal cirri. Dorsal cilia *c.* 3–4 μm long.

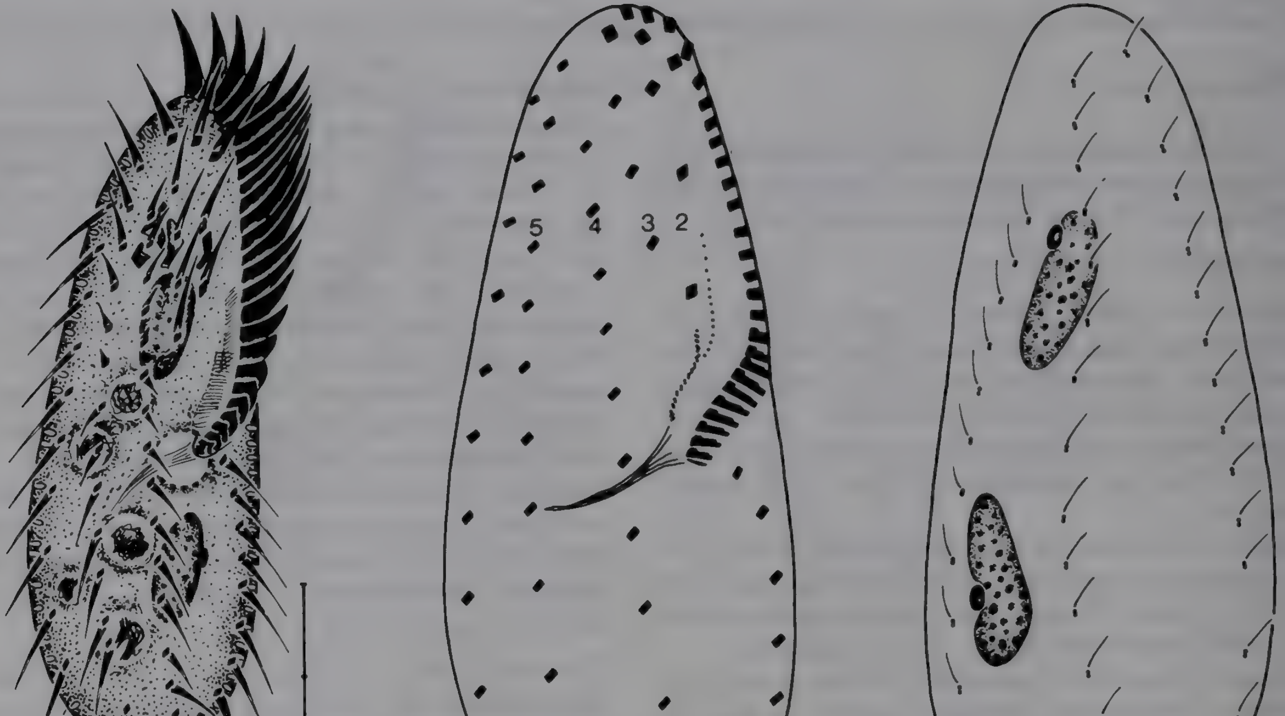
COMPARISON WITH RELATED SPECIES. The new species can be distinguished from *Birojimia muscorum* by the lack of subpellicular granules and the distinctly higher number of right marginal rows (Kahl, 1932; Foissner, 1982).

Wallackia bujoreani (Lepsi, 1951) nov. comb.
(basionym: ***Paraholosticha bujoreani*** Lepsi, 1951)

REDESCRIPTION (Figs 19–22, Tables 1, 5). *In vivo* about 70 × 25 μm, ellipsoid, body margins converging anteriad, both ends rounded. Macronuclear segments lying distinctly left of the median, with small chromatin bodies and adjacent micronuclei. Contractile vacuole in about the middle of the cell, distinctly displaced inwards, positioned dorsally at the level of the proximal part of the adoral zone of membranelles.



Figs 16–18 *Birojimia terricola* from life (Fig. 16) and after protargol impregnation (Figs 17, 18). **16** Ventral view. **17, 18** Infraciliature in ventral and dorsal view. 1–6, right marginal rows 1–6.



Figs 19–22 *Wallackia bujoreani* from life (Figs 19, 20) and after protargol impregnation (Figs 21, 22). **19** Ventral view. **20** Colourless, short ellipsoid extrusomes close beneath the pellicle. **21, 22** Infraciliature in ventral and dorsal view. 2–5, frontoventral rows 2–5.

Table 5 Biometrical characterization of *Wallackia bujoreani*

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	67.4	67.0	7.7	2.309	11.4	52.0	80.0	11
Body, width	24.4	22.0	5.1	1.527	20.8	17.0	36.0	11
Adoral membranelles, number	25.3	25.0	1.4	0.407	5.3	23.0	27.0	11
Adoral zone of membranelles, length	33.8	35.0	3.3	0.980	9.6	25.0	36.0	11
Macronuclear segments, number	2.0	2.0	0	0	0	2.0	2.0	11
Posterior macronuclear segment, length	12.4	12.0	2.0	0.607	16.3	10.0	17.0	11
Posterior macronuclear segment, width	4.7	4.0	1.0	0.304	21.3	4.0	7.0	11
Micronuclei, number	2.0	2.0	0	0	0	2.0	2.0	11
Posterior micronucleus, length	2.6	3.0	0.5	0.161	20.3	1.8	3.0	11
Posterior micronucleus, width	1.4	1.5	0.3	0.091	21.4	1.0	2.0	11
Left marginal row, number of cirri	8.9	9.0	0.8	0.251	9.3	8.0	10.0	11
Right marginal row, number of cirri	10.5	10.5	1.1	0.342	10.3	9.0	12.0	10
Frontal cirri, number	3.0	3.0	0	0	0	3.0	3.0	9
Frontoventral rows, number[1]	4.0	4.0	0	0	0	4.0	4.0	11
Frontoventral row 2, number of cirri[1]	2.2	2.0	0.4	0.133	19.2	2.0	3.0	10
Frontoventral row 3, number of cirri[1]	3.0	3.0	0.5	0.149	15.7	2.0	4.0	10
Frontoventral row 4, number of cirri[1]	11.8	12.0	1.4	0.423	11.9	10.0	14.0	11
Frontoventral row 5, number of cirri[1]	13.2	13.0	1.3	0.377	9.5	11.0	15.0	11
Caudal cirri, number	3.0	3.0	0	0	0	3.0	3.0	7
Dorsal kineties, number	3.0	3.0	0	0	0	3.0	3.0	11

[1] For the designation of the frontoventral rows see Figure 21. Frontoventral row 1 is not included.

Table 6. Biometrical characterization of *Laurentiella strenua*

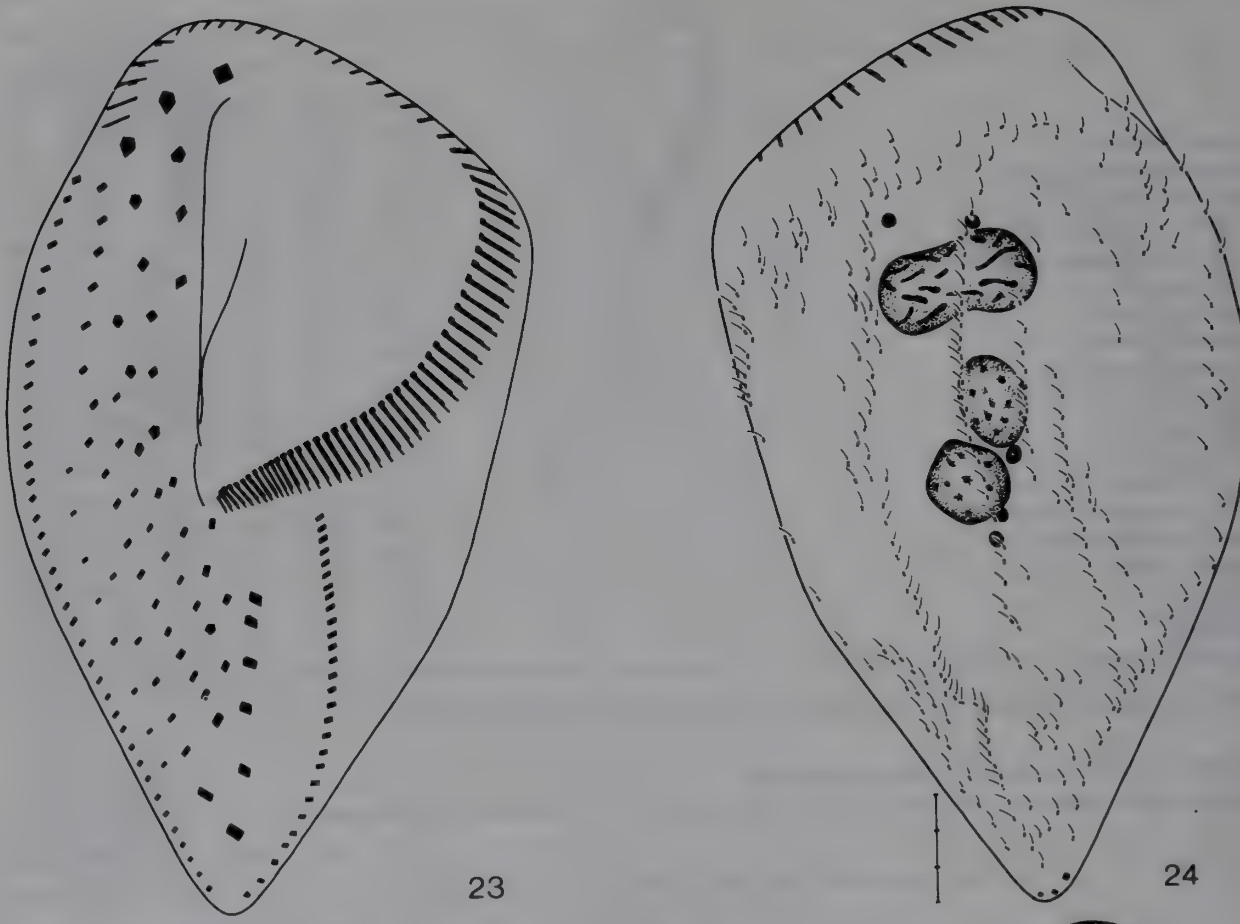
Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	268.6	260.0	28.7	8.651	10.7	240.0	325.0	11
Body, width	159.6	155.0	16.6	4.995	10.4	140.0	196.0	11
Adoral membranelles, number	65.8	65.0	1.9	0.569	2.9	64.0	70.0	11
Adoral zone of membranelles, length	134.3	130.0	9.5	2.870	7.1	120.0	150.0	11
Macronuclear segments, number	4.6	4.0	1.8	0.529	38.6	2.0	7.0	11
Posterior macronuclear segment, length	36.1	32.0	11.7	3.541	32.5	20.0	56.0	11
Posterior macronuclear segment, width	22.4	22.0	6.6	1.974	29.3	11.0	32.0	11
Micronuclei, number	7.5	6.0	7.1	2.129	94.7	2.0	24.0	11
Posterior micronucleus, length	3.8	3.5	0.7	0.223	19.3	3.0	5.6	11
Posterior micronucleus, width	3.5	3.5	0.4	0.126	11.8	3.0	4.2	11
Left marginal row, number of cirri	28.8	29.0	1.7	0.501	5.8	27.0	32.0	11
Right marinal row, number of cirri	39.7	40.0	1.9	0.574	4.8	37.0	42.0	11
Frontal cirri, number	3.0	3.0	0	0	0	3.0	3.0	11
Frontoventral rows (including buccal row), number	5.8	6.0	0.9	0.263	15.0	5.0	7.0	11
Transverse cirri, number	5.6	5.0	0.8	0.244	14.4	5.0	7.0	11
Caudal cirri, number	3.0	3.0	0	0	0	3.0	3.0	11

Extrusomes colourless, c. 1.5 µm in diameter, ellipsoid, irregularly arranged, impregnate with protargol. Cytoplasm colourless, with some yellowish, *c.* 4 µm large cytoplasmic crystals and some food vacuoles (5–7 µm in diameter) containing bacteria. Rapid jerky movement, sometimes becoming stationary for a moment.

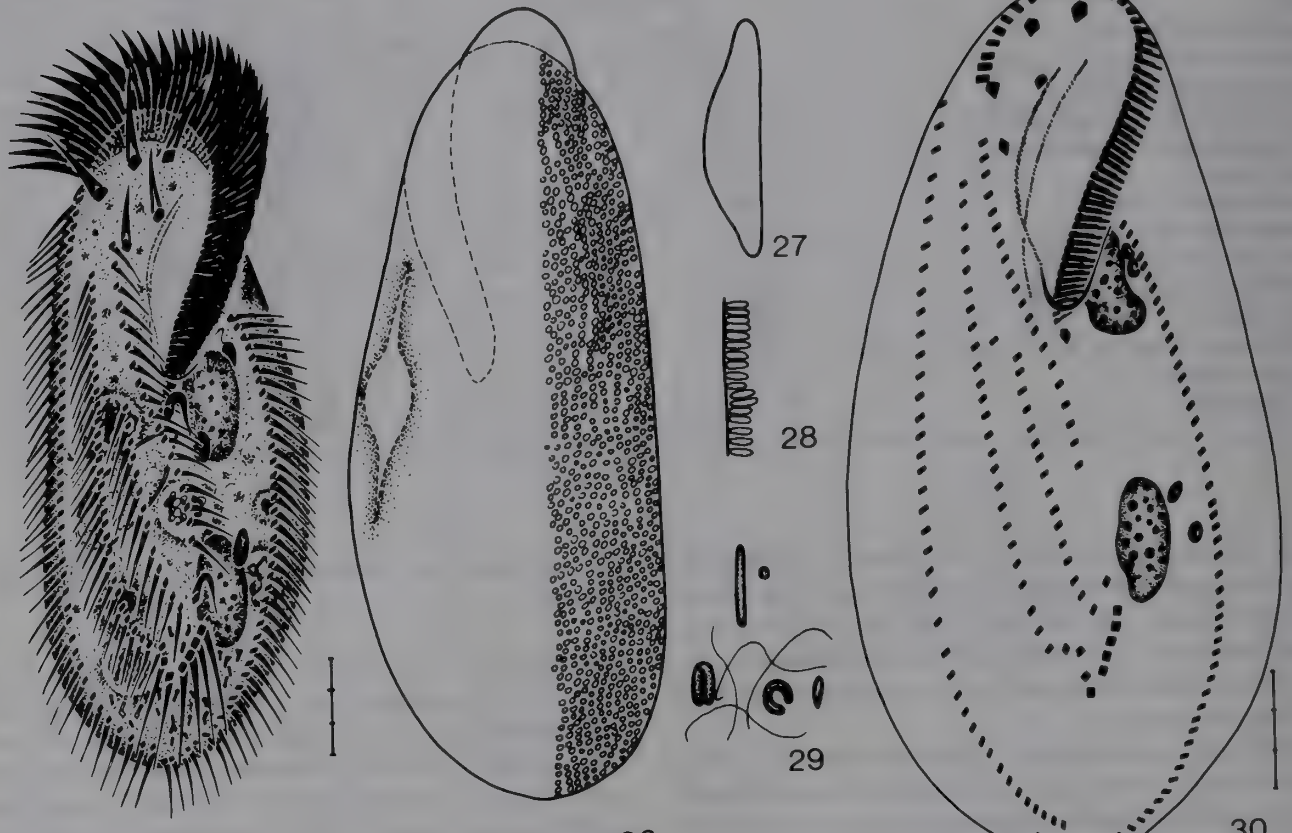
Adoral zone of membranelles '*Gonostomum*-like', about 50 % of body length, bases of the largest membranelles *in vivo c.* 4 µm wide. Undulating membranes short, the anterior (endoral ?) one consists of loosely arranged basal bodies. Anteriormost cirrus of the frontoventral rows 1–3 slightly enlarged. Frontoventral rows 2 and 3 restricted to the frontal area, frontoventral rows 4 and 5 about body length, the posterior 2 cirri of each row slightly separated. Right marginal row shorter than the frontoventral row 5, marginal cirri *in vivo c.* 12 µm long. Dorsal kinety 1 slightly shortened anteriorly, dorsal cilia *in vivo c.* 4 µm long. Caudal cirri conspicuous, *in vivo* about 20 µm long, 1 cirrus on each dorsal kinety.

COMPARISON WITH RELATED SPECIES. The body shape, the ventral infraciliature, the extrusomes, and the habitat of our population agree very well with the original description of Lepsi (1951), which is, however, based on living observations only. *Wallackia bujoreani* differs from the limnetic species *W. schiffmanni* Foissner, 1976 by the lower number of cirri in the frontoventral rows 2 and 3 and the lower number of dorsal kineties as well as in the shape and size of the extrusomes.

Wallackia Foissner, 1976 is probably closely related to the genus *Kahliella* Corliss, 1960, which has a very similiar arrangement of the 5 frontoventral rows but no caudal cirri (Berger & Foissner 1987, 1988c). A close relationship to *K. acrobates* (Horváth, 1932) Corliss, 1960 was already mentioned by Lepsi (1951). *Wallackia* differs from



Figs 23, 24 *Laurentiella strenua*. Infraciliature in ventral and dorsal view after protargol impregnation.



Figs 25–30 *Paraurostyla granulifera* from life (Figs 25–28), after methylgreen-pyronin staining (Fig. 29), and after protargol impregnation (Fig. 30). **25–27** Ventral, dorsal, and lateral view. The right side of Figure 26 shows the arrangement of the colourless subpellicular granules. **28, 29** Extrusomes. **30** Infraciliature in ventral view.

Table 7 Biometrical characterization of *Paraurostyla granulifera*

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	211.9	204.0	17.4	6.592	8.2	195.0	240.0	7
Body, width	92.7	92.0	12.7	4.804	13.7	70.0	112.0	7
Adoral membranelles, number	59.9	60.0	3.2	1.223	5.4	55.0	65.0	7
Adoral zone of membranelles, length	84.0	84.0	5.4	2.035	6.4	73.0	90.0	7
Macronuclear segments, number	2.0	2.0	0	0	0	2.0	2.0	7
Macronuclear segments, distance between	35.0	35.0	4.4	3.651	12.5	27.0	39.0	7
Posterior macronuclear segment, length	26.1	24.0	4.0	1.519	15.4	22.0	34.0	7
Posterior macronuclear segment, width	13.9	14.0	0.9	0.340	6.5	13.0	15.0	7
Micronuclei, number	4.1	4.0	1.1	0.404	25.8	3.0	6.0	7
Posterior micronucleus, length	5.8	6.0	0.9	0.341	15.5	4.0	7.0	7
Posterior micronucleus, width	3.4	3.0	0.5	0.202	15.6	3.0	4.0	7
Left marginal row, number of cirri	48.0	47.0	5.3	1.988	11.0	40.0	56.0	7
Right marginal row, number of cirri	40.0	40.0	1.8	0.690	4.6	38.0	43.0	7
Frontal cirri, number	3.0	3.0	0	0	0	3.0	3.0	7
Buccal cirri, number	1.0	1.0	0	0	0	1.0	1.0	7
Cirri behind the right frontal cirrus, number	1.0	1.0	0	0	0	1.0	1.0	7
Frontoventral rows, number	3.0	3.0	0	0	0	3.0	3.0	7
Left frontoventral row, number of cirri	18.3	19.0	2.4	0.918	13.3	15.0	22.0	7
Middle frontoventral row, number of cirri	14.0	13.0	2.0	0.756	14.3	12.0	18.0	7
Right frontoventral row, number of cirri	31.1	30.0	1.7	0.634	5.4	30.0	34.0	7
Postoral ventral cirri, number	1.4	1.0	0.5	0.202	37.4	1.0	2.0	7
Ventral cirri near the transverse cirri, number	2.0	2.0	0	0	0	2.0	2.0	7
Transverse cirri, number	7.0	7.0	0.6	0.218	8.2	6.0	8.0	7
Distance 1[1]	30.0	28.0	6.7	2.562	22.3	21.0	39.0	7
Caudal cirri, number	3.0	3.0	0	0	0	3.0	3.0	7

[1] Distance 1, distance between the posterior transverse cirrus and the posterior end of the cell.

Trachelochaeta Šrámek-Hušek, 1954 by the lack of distinct transverse cirri.

Laurentiella strenua (Dingfelder, 1962) nov. comb. (basionym: ***Paruroleptus strenuus*** Dingfelder, 1962)

Discussion and additional observations (Figs 23, 24, Tables 1, 6). Neither Fedriani *et al.* (1976) nor Martin *et al.* (1983) compared *L. acuminata* (Fedriani, Martin & Perez-Silva, 1976) with *Paruroleptus strenua* described by Dingfelder (1962) and redescribed by Czapik & Jordan (1976). There are some differences between the descriptions of *L. acuminata* and *L. strenua*, as in the number of macronuclear segments and frontoventral rows. However, both characters show a high variability (see Table 6), which suggests that they should not be used to separate species. Thus, in our opinion *L. acuminata* is a junior synonym of *L. strenua*.

The generic classification of this conspicuous species is still uncertain and can probably be discussed successfully only after the description of the type-species of the closely related genus *Onychodromus* Stein, 1859, *O. grandis* Stein, 1859 (Stein 1859*a,b*; Foissner *et al.*, 1987; Foissner, unpublished).

Here we give a biometrical characterization and line drawings of the ventral and dorsal infraciliature of the type-population of *L. acuminata*, kindly supplied by Dr J. Martin (University of Cordoba, Spain).

Paraurostyla granulifera nov. spec.

Diagnosis. *In vivo* 170–230 × 70–100 μm. Perpendicular to the pellicle very many *c.* 2 × 1 μm large, colourless subpellicular granules (extrusomes). 60 adoral membranelles and 7 considerably anteriad displaced transverse cirri on average. 3 frontoventral rows, 1–2 postoral ventral cirri.

Type location. Soil of a deciduous forest. Mt Ryu-Ga-Take, Amakusa, Kumamoto Prefecture, Japan.

Description (Figs 25–30, Tables 1, 7). Right margin straight, left one convex, in the anterior part markedly indented. Anterior and posterior end rounded. About 2:1 flattened, body flexible. Macronuclear segments lying distinctly left of the median of the cell. Micronuclei *in vivo c.* 7 × 5 μm. Contractile vacuole in about the middle of the cell, during diastole with channels. Single extrusomes are difficult to discern, because they are very closely spaced, forming a distinct lucident seam, which gives the organism a brownish colour at low magnification. Extrusomes ejected after the addition of methylgreen-pyronin, stain red, u- or horseshoe-shaped; between this type of extrusomes there are many thin structures which are probably fully exploded extrusomes. Cytoplasm colourless, with many cytoplasmatic crystals and food vacuoles with fungal spores, flagellates, cysts of amoebae, and testaceans (*Trinema enchelys*). Rapid movement.

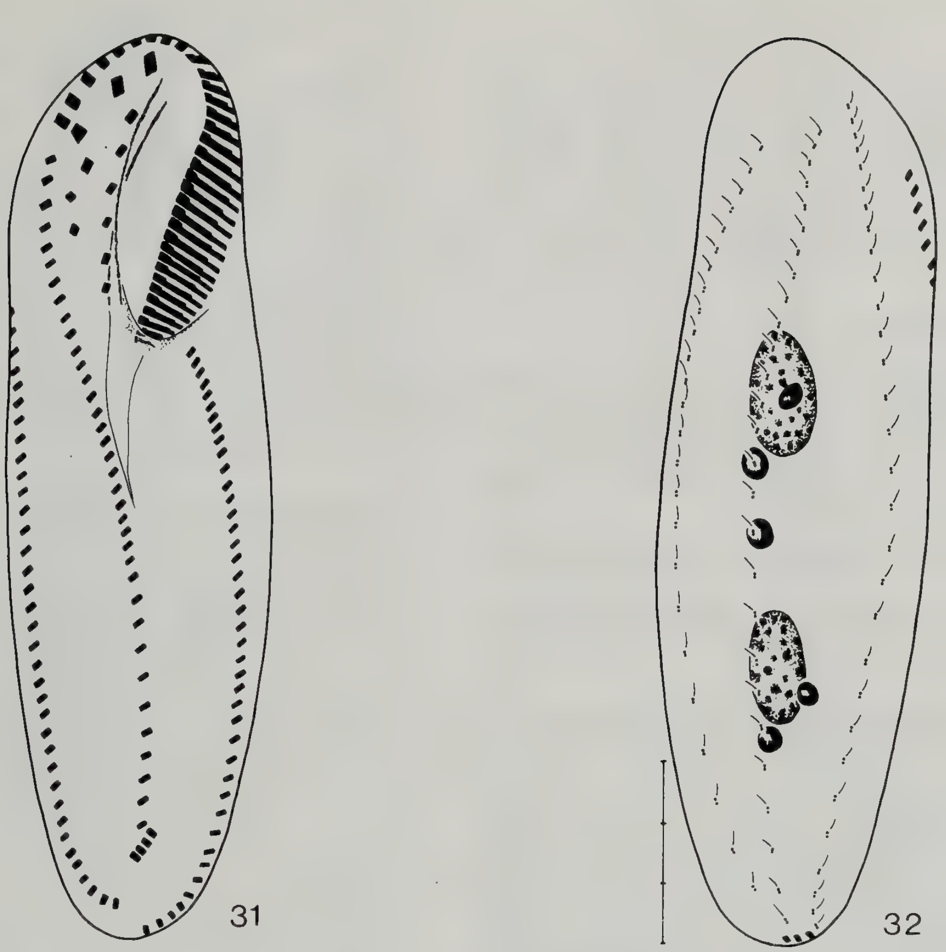
Adoral zone of membranelles about 40% of body length, bases of the largest membranelles *in vivo c.* 8 μm wide. Undulating membranes slightly bent, nearly of the same length, paroral membrane consists of short oblique kineties, at least in the middle part. Buccal cirrus near the anterior end of the paroral membrane. Bases of the buccal cirrus, the cirrus behind the right frontal cirrus, and the *in vivo c.* 25 μm long frontal cirri distinctly enlarged. Left and right frontoventral row begin at the level of the cirrus behind the right frontal cirrus, the left one terminates in about the middle of the cell, the right one at the transverse cirri like the middle row, which begins at about the level of the cytostome. Transverse cirri *in vivo c.* 30 μm long, terminate at the posterior edge of the cell. Marginal rows nearly confluent posteriorly, cirri *in vivo c.* 20 μm long. 3 caudal cirri at the

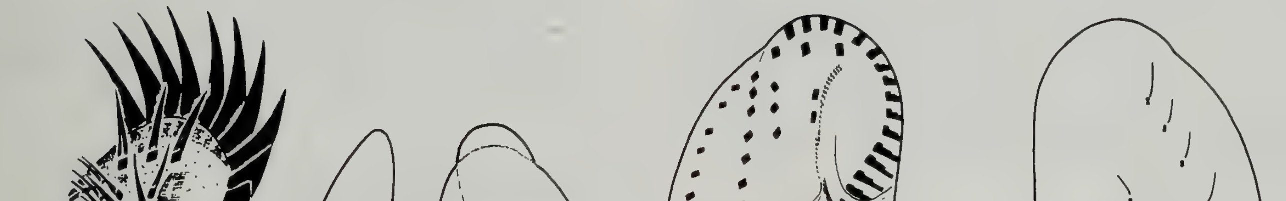
Table 8 Biometrical characterization of *Amphisiella polycirrata* (upper line), *Amphisiella quadrinucleata* (middle line), and *Uroleptoides binucleata* (lower line)

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	150.0	150.0	10.0	5.774	6.7	140.0	160.0	3
	86.3	84.0	10.1	2.607	11.7	70.0	105.0	15
	140.6	140.0	12.7	4.014	9.0	126.0	168.0	10
Body, width	46.7	46.0	5.0	2.906	10.8	42.0	52.0	3
	25.2	25.0	3.1	0.812	12.5	21.0	32.0	15
	40.9	41.0	6.0	1.900	14.7	35.0	50.0	10
Adoral membranelles, number	36.7	37.0	1.5	0.882	4.2	35.0	38.0	3
	16.6	17.0	1.6	0.412	9.6	14.0	19.0	15
	24.5	24.0	1.8	0.627	7.2	22.0	28.0	8
Adoral zone of membranelles, length	52.7	56.0	5.8	3.333	11.0	46.0	56.0	3
	18.3	19.0	2.5	0.645	13.6	14.0	22.0	15
	29.4	30.0	1.3	0.400	4.3	28.0	31.0	10
Macronuclear segments, number	2.0	2.0	0	0	0	2.0	2.0	3
	4.0	4.0	0	0	0	4.0	4.0	15
	2.0	2.0	0	0	0	2.0	2.0	9
Posterior macronuclear segment, length	19.3	21.0	3.8	2.186	19.6	15.0	22.0	3
	8.1	8.0	1.0	0.256	12.2	7.0	10.0	15
	25.2	25.0	3.8	1.209	15.2	20.0	31.0	10
Posterior macronuclear segment, width	10.7	11.0	0.6	0.333	5.4	10.0	11.0	3
	5.5	6.0	0.6	0.165	11.7	4.0	6.0	15
	8.0	8.0	0.9	0.298	11.8	7.0	10.0	10
Macronuclear segments, distance between[1]	25.7	25.0	2.1	1.202	8.1	24.0	28.0	3
	7.5	7.0	2.5	0.646	33.5	4.0	14.0	15
	–	–	–	–	–	–	–	0
Distance 1[2]	–	–	–	–	–	–	–	0
	3.7	3.0	1.9	0.494	52.2	0	7.0	15
	–	–	–	–	–	–	–	0
Micronuclei, number	3.7	3.0	1.2	0.667	31.5	3.0	5.0	3
	2.3	2.0	0.5	0.125	20.5	2.0	3.0	14
	2.0	2.0	0	0	0	2.0	2.0	9
Posterior micronucleus, length	4.0	4.0	0.5	0.289	12.5	3.5	4.5	3
	1.8	1.6	0.6	0.168	34.4	1.4	3.5	14
	5.6	6.0	1.1	0.340	19.2	4.0	7.0	10
Posterior micronucleus, width	3.4	3.5	0.6	0.348	17.6	2.8	4.0	3
	1.7	1.5	0.6	0.151	33.9	1.4	3.0	14
	2.8	3.0	0.5	0.167	18.6	2.0	4.0	10
Left marginal row, number of cirri	41.0	44.0	9.9	5.686	24.0	30.0	49.0	3
	36.6	35.0	6.1	1.579	16.7	29.0	49.0	15
	46.0	45.0	5.1	1.793	11.0	42.0	58.0	8
Right marginal row, number of cirri	43.0	44.0	6.7	3.786	15.2	36.0	49.0	3
	36.1	36.0	2.8	0.714	7.7	32.0	41.0	15
	42.3	42.5	3.3	1.652	7.8	38.0	46.0	4
Frontal cirri, number	3.0	3.0	0	0	0	3.0	3.0	3
	3.0	3.0	0	0	0	3.0	3.0	15
	3.0	3.0	0	0	0	3.0	3.0	5
Buccal cirri, number	5.3	6.0	1.2	0.667	21.7	4.0	6.0	3
	2.7	3.0	0.5	0.118	16.7	2.0	3.0	15
	1.0	1.0	0	0	0	1.0	1.0	7
Left frontoventral row, number of cirri	3.0	3.0	0	0	0	3.0	3.0	3
	3.2	3.0	0.4	0.107	12.9	3.0	4.0	15
	2.8	3.0	0.8	0.375	29.9	2.0	4.0	5
Right frontoventral row, number of cirri	32.5	32.5	6.4	4.500	19.6	28.0	37.0	2
	14.6	15.0	1.6	0.423	11.2	12.0	18.0	15
	22.3	23.0	1.5	0.615	6.7	20.0	24.0	6
Distance 2[2]	–	–	–	–	–	–	–	0
	11.7	11.0	2.3	0.599	19.9	7.0	15.0	15
	–	–	–	–	–	–	–	0
Distance 3[2]	–	–	–	–	–	–	–	0
	32.5	32.0	3.9	1.018	12.1	25.0	39.0	15
	83.7	82.0	8.2	3.353	9.8	75.0	98.0	6
Transverse cirri, number	4.0	4.0	0	0	0	4.0	4.0	2
	3.0	3.0	0.4	0.098	12.6	2.0	4.0	15
	4.0	4.0	0	0	0	4.0	4.0	7
Dorsal kineties, number	3.0	3.0	0	0	0	3.0	3.0	3
	2.0	2.0	0	0	0	2.0	2.0	15
	3.0	–	–	–	–	–	–	1

[1] In *A. quadrinucleata* the distance between the second and the third macronuclear segment is listed.

[2] Distance 1, distance between the first and the second macronuclear segment. Distance 2, distance 3, distance between the anterior end of the cell and the posterior end of the left and right frontoventral row, respectively.





Figs 31, 32 *Amphisiella polycirrata*. Infraciliature in ventral and dorsal view after protargol impregnation.

Figs 33–37 *Amphisiella quadrinucleata* from life (Figs 33–35) and after protargol impregnation (Figs 36, 37). **33–35** Ventral, lateral, and dorsal view. **36, 37** Infraciliature in ventral and dorsal view.

posterior end of the cell. The dorsal infraciliature was hidden by the extrusomes which often stain with protargol.

COMPARISON WITH RELATED SPECIES. The ventral infraciliature of *P. granulifera* is very similar to that of *P. fossicola* (Kahl, 1932) Borror, 1972. This fresh-water species, however, has obviously no subpellicular granules (extrusomes), because Kahl (1932), who studied it in great detail, did not mention them. The extrusomes of our species are so conspicuous that we can hardly imagine that Kahl (1932) overlooked them.

Amphisiella polycirrata nov. spec.

DIAGNOSIS. After protargol impregnation about 150 × 46 µm, long ellipsoid. 2 macronuclear segments, 3 dorsal kineties. 6 buccal cirri, 4 transverse cirri, and 37 adoral membranelles on average. About 33 cirri in the right frontoventral row which terminates at the transverse cirri.

TYPE LOCATION. Soil from Garajan Kap, Madeira, Portugal.

DESCRIPTION (Figs 31, 32, Tables 1, 8). Only a few specimens were found in the slides, thus the biometric characterization is incomplete.

Both ends rounded. Macronuclear segments lying almost in the median of the cell, with many small chromatin bodies. Subpellicular granules absent. Feeds on flagellates and ciliates.

Adoral zone of membranelles about 35% of body length. Buccal area large and deep. Undulating membranes slightly bent, of about the same length. Bases of the 3 frontal cirri distinctly enlarged. Right frontoventral row begins near the distal end of the adoral zone of membranelles, always terminates very near to the transverse cirri; the bases of the 3 anteriormost cirri of this row are slightly enlarged. Dorsal cilia 3 µm long. It could not be clarified whether the 3 cirri shown in Figure 32 are caudal cirri or the posteriormost cirri of the left marginal row.

COMPARISON WITH RELATED SPECIES. *In vivo* this species looks so similar to *Amphisiella terricola* Gellért, 1955, that we considered it unnecessary to draw the living aspect. However, the ventral infraciliature of the new species differs from that of *A. terricola* in the number of buccal cirri, transverse cirri, and adoral membranelles and by having a frontoventral row which terminates at the transverse cirri (Gellért, 1955; Foissner, 1984).

Amphisiella polycirrata can be distinguished from *A. quadrinucleata* and the species mentioned in the discussion of *A. quadrinucleata* (see below) by the number of buccal cirri, dorsal kineties, and macronuclear segments.

Amphisiella quadrinucleata nov. spec.

DIAGNOSIS. *In vivo* about 100–125 × 30 µm, long ellipsoid. 4 macronuclear segments, 2 dorsal kineties, 2–3 buccal cirri. 15 cirri in the right frontoventral row, 3 transverse cirri, and 17 adoral membranelles on average.

TYPE LOCATION. Soil from Mae-Shima, Amakusa, Kumamoto Prefecture, Japan.

DESCRIPTION (Figs 33–37, Tables 1, 8). Body margins parallel, anterior part of the cell usually bent to the left. Both ends rounded. About 2:1 flattened, flexible. Macronuclear segments *in vivo c.* 10 × 6 µm, with large chromatin bodies, lying slightly left of the median. Contractile vacuole slightly above the middle of the cell, distinctly displaced inwards, during diastole without channels. Subpellicular granules absent. Cytoplasm colourless, with numerous 1–7 µm large, fat globules and some food vacuoles containing ciliates (*Colpoda fastigata, Pseudoplatyophrya nana*). Slow movement, trembling.

Adoral zone of membranelles 20% of body length. Undulating membranes slightly bent, about the same length, superimposed or closely arranged side by side. Frontal cirri slightly enlarged. Left frontoventral row short, behind the right frontal cirrus. Right row terminates at 38% of body length on average. Marginal cirri *in vivo c.* 10 µm, transverse cirri *c.* 14 µm long, the latter protrude distinctly beyond the posterior edge of the cell. Dorsal cilia *in vivo c.* 3 µm long, kinety 1 slightly shortened anteriorly, in kinety 2 the distances between the basal body pairs become wider in the posterior direction. Caudal cirri absent.

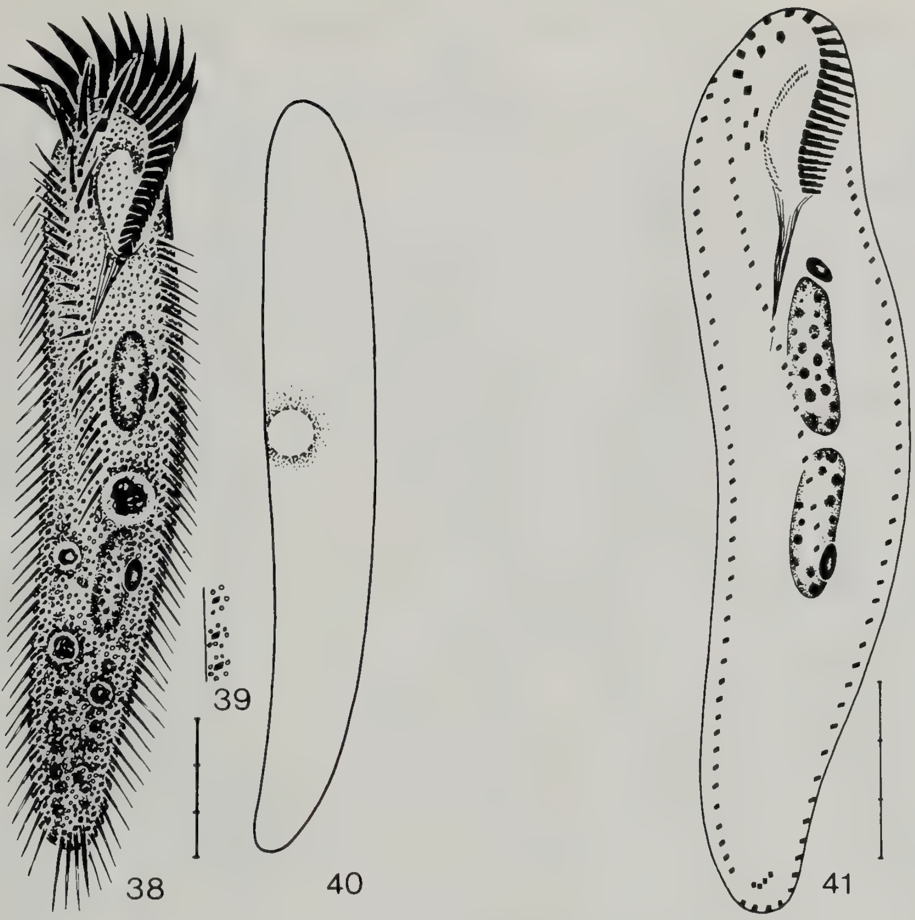
COMPARISON WITH RELATED SPECIES. The new species is classified in the genus *Amphisiella* Gourret & Roeser, 1888, because it has a distinct frontal row, transverse cirri, and a dorsal infraciliature which consists of dorsal kineties only (caudal cirri absent). This agrees largely with the type-species *A. marioni* Gourret & Roeser, 1888 as redescribed by Wicklow (1982). *Amphisiella quadrinucleata* can be distinguished from the type-species and the other congeneric species listed by Borror (1972), *A. raptans* Buitkamp & Wilbert, 1974; *A. acuta* Foissner, 1982; and *A. oscensis* Fernandez-Leborans, 1984, by the body shape, the body size, the number of macronuclear segments, transverse cirri, and dorsal kineties. The ventral and dorsal infraciliature of *A. quadrinucleata* is similar to the species of the genus *Lamtostyla* Buitkamp, 1977*a*, too. In this genus, however, the frontoventral cirri are restricted to the area right of the buccal cavity (Berger & Foissner, 1988*a*).

Uroleptoides binucleata Hemberger, 1985

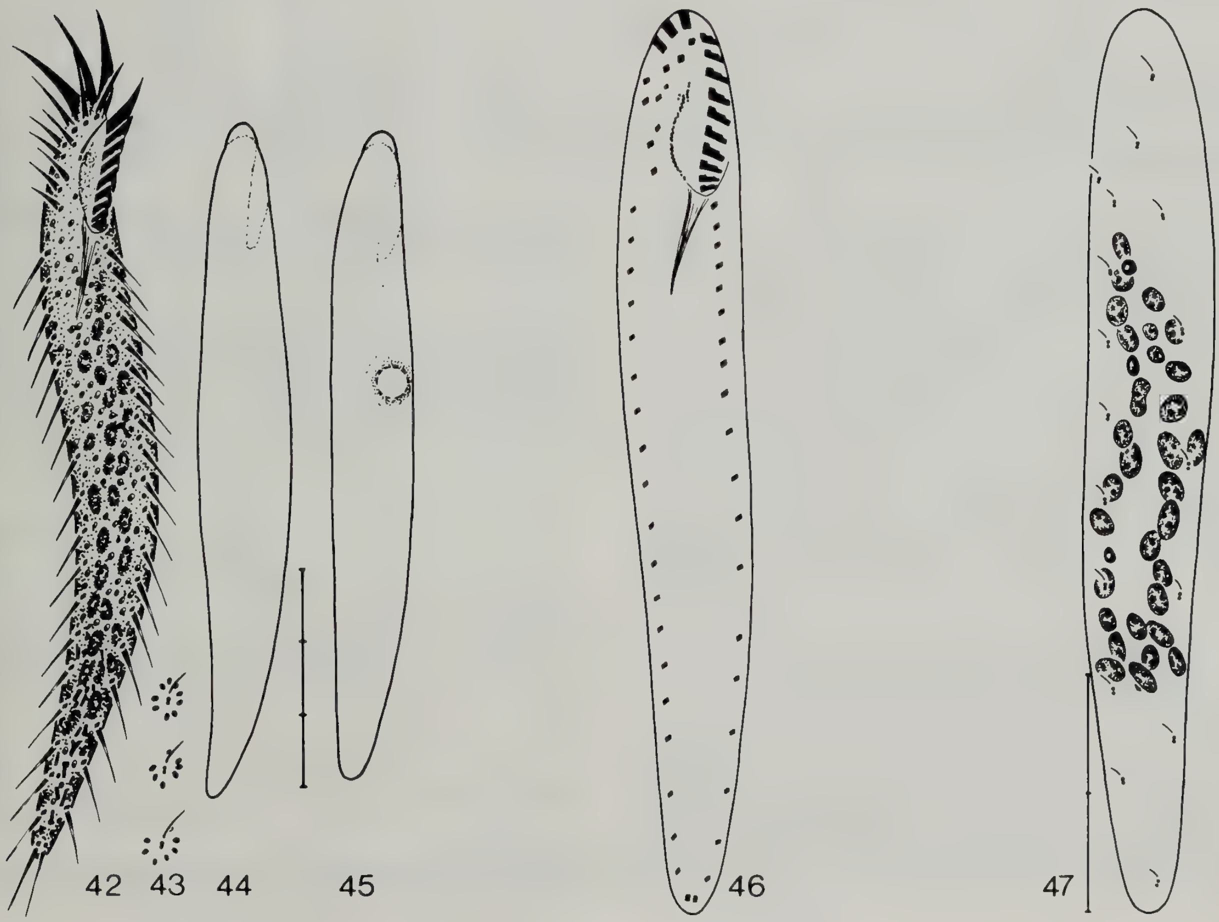
REDESCRIPTION (Figs 38–41, Tables 1, 8). Body often slightly twisted, very flexible, inconspicuously flattened, margins converging posteriorly, both ends rounded. Macronuclear segments long ellipsoid, lying almost in the median of the cell. Micronuclei *in vivo* c. 7 × 4 µm. Contractile vacuole slightly above the middle of the cell. Around the bases of the cirri and in the buccal area inconspicuous (< 1 µm) colourless granules, which do not stain with methylgreen-pyronin. Cytoplasm colourless, densely granulated, posteriorly many about 3 µm large yellowish fat globules. Probably feeds on zooflagellates. Rapid movement.

Adoral zone of membranelles *c.* 20% of body length, bases of the largest membranelles *in vivo c.* 6 µm wide. Undulating membrances distinctly bent, pharyngeal fibres *in vivo* conspicuous. Frontal cirri enlarged. Buccal cirrus inserted slightly behind the middle of the undulating membranes. Frontoventral row terminates at 60% of body length. Marginal cirri *in vivo c.* 12 µm, transverse cirri *c.* 20 µm, and dorsal cilia *c.* 3 µm long. Dorsal infraciliature poorly stained, probably 3 kineties (1 specimen).

DISCUSSION The body shape, the nuclear apparatus, the ventral cirral pattern, and the number of adoral membranelles of our population from Berlin, FRG, agree very well with the type-material which was found in a mull-rendsina soil near Bonn, FRG. Differences exist in the body size (type-material 200–260 × 50 µm; our population 160–180 × 30 µm) and consequently in the number of right (60; 38–46) and left



Figs 38–41 *Uroleptoides binucleata* from life (Figs 38–40) and after protargol impregnation (Fig. 41). **38** Ventral view. **39** Small (< 1 μm), colourless subpellicular granules around the bases of the cirri. **40** Dorsal view. **41** Infraciliature in ventral view.



Figs 42–47 *Hemisincirra inquieta* from life (Figs 42–45) and after protargol impregnation (Figs 46, 47). **42** Ventral view. **43** Ellipsoid, about 1 μm large, orange-yellow subpellicular granules around the bases of the dorsal cilia. **44, 45** Ventral views. **46, 47** Infraciliature in ventral and dorsal view.

Table 9 Biometrical characterization of *Hemisincirra inquieta* (upper line), *Hemisinicirra vettersi* (middle line), and *Terricirra matsusakai* (lower line)

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	84.6	90.0	11.4	4.298	13.4	70.0	98.0	7
	143.6	145.0	18.6	5.162	13.0	112.0	180.0	13
	93.2	95.0	11.2	3.379	12.0	78.0	112.0	11
Body, width	12.6	13.0	1.3	0.481	10.1	11.0	14.0	7
	12.0	11.0	1.5	0.424	12.7	10.0	15.0	13
	23.9	23.0	5.3	1.592	22.1	18.0	35.0	11
Adoral membranelles, number	13.1	13.0	0.7	0.261	5.3	12.0	14.0	7
	8.3	8.0	0.6	0.175	7.6	7.0	9.0	13
	18.2	18.0	1.3	0.377	6.9	16.0	20.0	11
Adoral zone of membranelles, length	15.1	15.0	1.4	0.508	8.9	13.0	17.0	7
	8.5	8.0	0.9	0.243	10.4	7.0	10.0	13
	17.5	17.0	1.2	0.366	6.9	15.0	20.0	11
Macronuclear segments, number	31.7	32.0	2.1	0.808	6.7	30.0	36.0	7
	27.5	27.0	7.5	2.074	27.2	20.0	50.0	13
	4.0	4.0	0	0	0	4.0	4.0	11
Posterior macronuclear segment, length	4.4	4.0	1.3	0.481	28.7	3.0	7.0	7
	9.2	7.0	4.9	1.372	54.0	3.0	22.0	13
	12.0	13.0	2.1	0.647	17.9	8.0	14.0	11
Posterior macronuclear segment, width	1.9	2.0	0.4	0.139	19.2	1.4	2.5	7
	1.8	1.7	0.4	0.102	21.0	1.2	2.5	13
	5.7	6.0	1.0	0.304	17.6	4.0	7.0	11
Micronuclei, number	2.1	2.0	0.7	0.261	32.2	1.0	3.0	7
	1.9	2.0	0.5	0.137	25.7	1.0	3.0	13
	1.9	2.0	0.8	0.251	43.5	1.0	3.0	11
Posterior micronucleus, length	2.3	2.5	0.5	0.187	21.8	1.6	2.8	7
	8.2	8.0	1.3	0.355	15.7	7.0	11.0	13
	1.6	1.6	0.0	0.012	2.6	1.5	1.6	11
Posterior micronucleus, width	1.6	1.5	0.1	0.052	8.8	1.4	1.8	7
	2.0	2.0	0.5	0.137	24.4	1.4	2.8	13
	1.6	1.6	0.0	0.012	2.6	1.5	1.6	11
Left marginal row, number of cirri	19.9	20.0	2.0	0.769	10.3	17.0	23.0	7
	52.1	53.0	4.7	1.313	9.1	43.0	60.0	13
	30.3	29.0	3.7	1.104	12.1	23.0	36.0	11
Right marginal row, number of cirri	21.4	21.0	2.3	0.869	10.7	18.0	2.0	7
	68.8	70.0	6.2	1.725	9.0	58.0	78.0	13
	32.2	32.0	4.4	1.327	13.7	26.0	41.0	11
Frontal cirri, number	3.0	3.0	0	0	0	3.0	3.0	7
	3.0	3.0	0	0	0	3.0	3.0	13
	3.0	3.0	0	0	0	3.0	3.0	11
Buccal cirri, number	1.3	1.0	0.8	0.333	61.2	1.0	3.0	7
	1.0	1.0	0	0	0	1.0	1.0	13
	1.0	1.0	0	0	0	1.0	1.0	11
Frontoventral row, number of cirri	–	–	–	–	–	–	–	0
	8.2	8.0	1.4	0.390	17.2	6.0	11.0	13
	4.0	4.0	0.5	0.135	11.2	3.0	5.0	11
Cirri left of the frontoventral row, number	–	–	–	–	–	–	–	0
	–	–	–	–	–	–	–	0
	1.1	1.0	0.3	0.091	27.6	1.0	2.0	11
Transverse cirri, number	2.0	2.0	0	0	0	2.0	2.0	6
	–	–	–	–	–	–	–	0
	3.2	3.0	0.6	0.180	19.0	3.0	5.0	11
Dorsal kineties, number[1]	3.0	3.0	0	0	0	3.0	3.0	7
	3.0	3.0	0	0	0	3.0	3.0	13
	4.0	4.0	0	0	0	4.0	4.0	11
Distance 1[2]	16.5	16.0	1.7	0.462	10.1	14.0	20.0	13

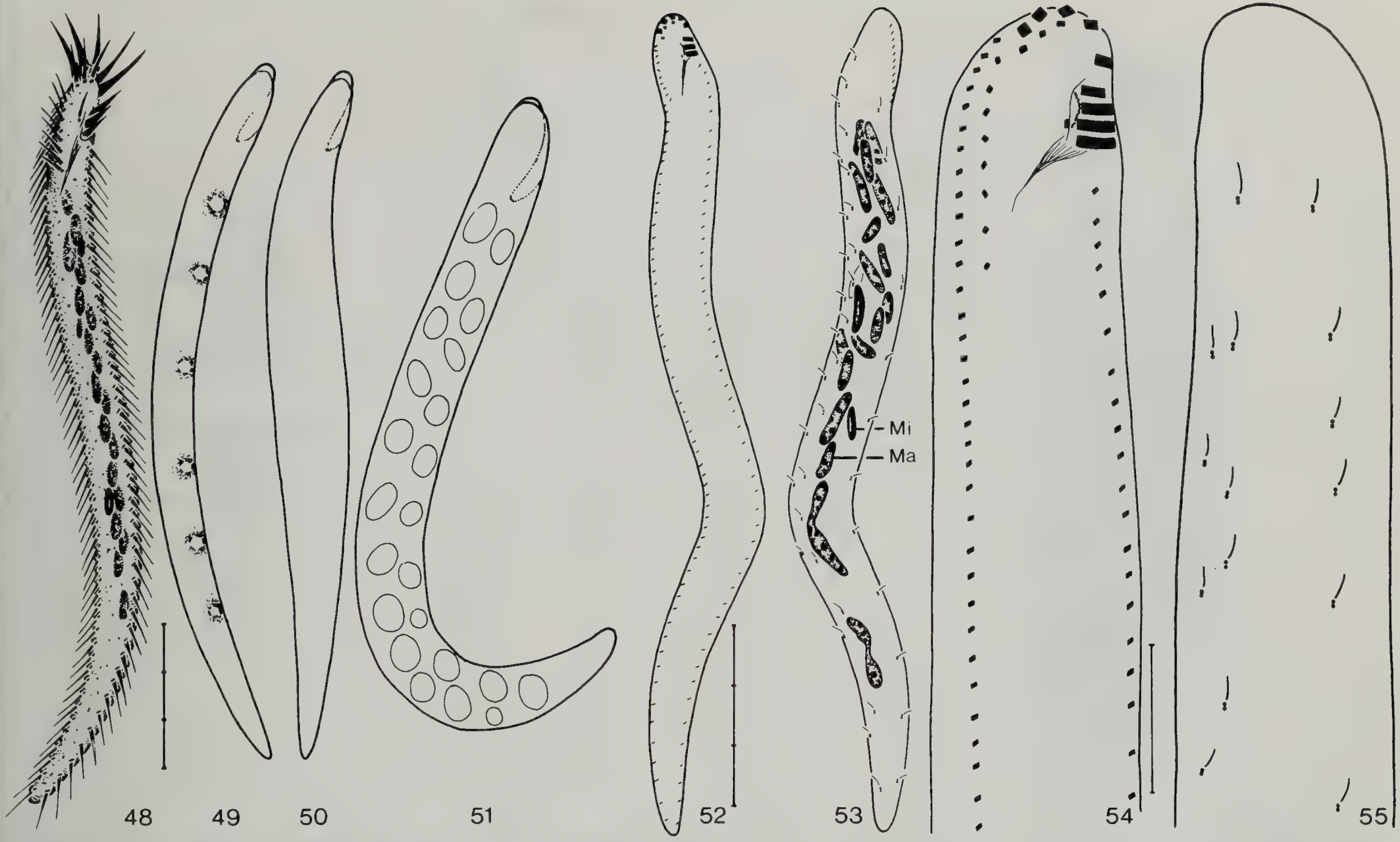
[1] In *H. inquieta* the single basal body pair (dorsal kinety 1, see Figure 47) is included.

[2] Distance 1, distance between the anterior end of the cell and the posterior end of the frontoventral row. These values are valid for *H. vettersi* only.

marginal cirri (55; 42–58) and cirri in the right frontoventral row (33–40; 20–24). Hemberger (1985) observed 3 terminal cirri (transverse cirri ?), whereas in the population from Berlin 4 distinct transverse cirri are recognizable. The granules around the cirri are not mentioned by Hemberger (1985). They are, in fact, rather difficult to discern and thus he may have overlooked them.

Hemisincirra inquieta Hemberger, 1985

DISCUSSION AND ADDITIONAL OBSERVATIONS (Figs 42–47, Tables 1, 9). The population from Iceland has a more tapered body shape than that from Ulm, FRG (Berger & Foissner 1987). However, the ventral and dorsal infraciliature and the



Figs 48–55 *Hemisincirra vettersi* from life (Figs 48–51) and after protargol impregnation (Figs 52–55). **48, 49** Theronts in ventral view. **50, 51** Trophonts in ventral view. **52–55** Infraciliature in ventral and dorsal view. Ma, macronuclear segment; Mi, micronucleus.

bio-metrical data agree very well with the type-material and the German population (Hemberger, 1985; Berger & Foissner, 1987).

In vivo about 115 × 15 µm, not flattened, very flexible. Subpellicular granules ellipsoid, about 1 µm long, orange-yellow, arranged around the cirri and dorsal cilia only. Cytoplasm with many *c.* 1 µm large, colourless fat granules. Vivacious movement.

Hemisincirra vettersi nov. spec.

Diagnosis. Theront *in vivo* about 150 × 9 µm, extremely vermiform. Trophont *in vivo* about 125–160 × 14–25 µm. About 6 contractile vacuoles near the left body margin. 27 macronuclear segments and 8 adoral membranelles on average. 3 dorsal kineties of body length.

Type location. Soil under a tuft of *Alchemilla alpina* near Dettifoss, Neisland, Iceland.

Dedication. This species is named in honour of Dr Wolfgang Vetters, University of Salzburg, who collected the soil samples from Iceland.

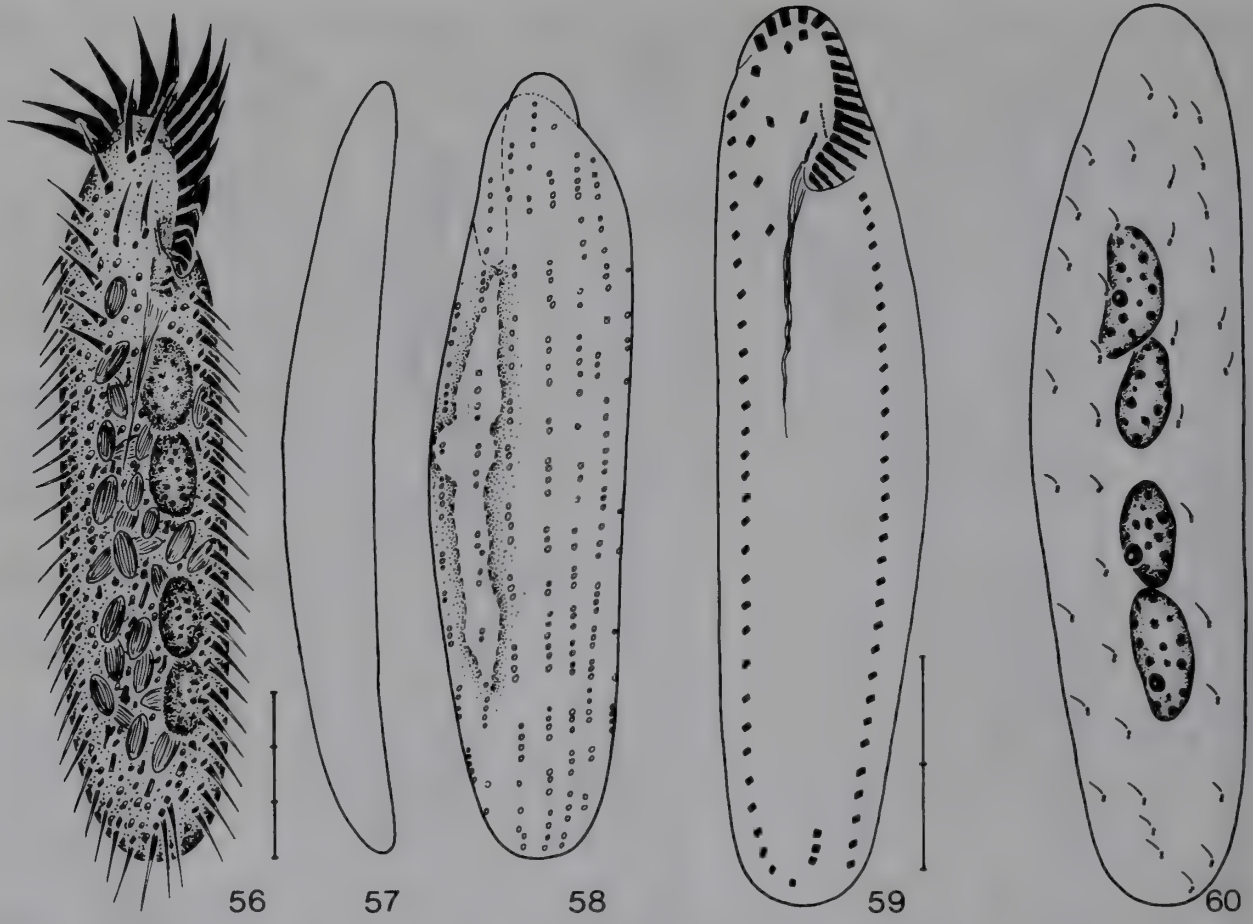
Description (Figs 48–55, Tables 1, 9). Theront usually s-shaped, posteriorly tapered. Trophont distinctly twisted, nematode-like. Frontal area very thin, remaining body not flattened, very fragile. Macronuclear segments and micronuclei usually elongated and of similar size. Subpellicular granules absent. Cytoplasm colourless, in trophonts with many about 10 µm large, fat globules. Theronts with worm-like movements, trophonts nearly motionless.

Adoral zone of membranelles about 6% of body length only! Distal adoral membranelles loosely arranged. Very probably the adoral membranelles consist of 2 rows of basal bodies only. Buccal area very small. Buccal cirrus inserted near the posterior end of the very small undulating membranes whose structures, thus, could not be seen clearly in the light microscope. All cirri very thin. Conspicuously more right than left marginal cirri. Transverse and caudal cirri very probably absent. Distance between dorsal kinety 1 and 2 distinctly smaller than between kineties 2 and 3.

Comparison with related species. *Hemisincirra vettersi* differs from the other vermiform congeneric species viz. *H. vermiculare* Hemberger, 1985; *H. interrrupta* (Foissner, 1982) Foissner, 1984; *H. filiformis* (Foissner, 1982) Foissner, 1984; *H. polynucleata* Foissner, 1984; and *H. muelleri* Foissner, 1986, in the number of dorsal kineties, adoral membranelles, macronuclear segments, and contractile vacuoles.

TERRICIRRA nov. gen.

Diagnosis. Vermiform to long ellipsoid Oxytrichidae with green to blue subpellicular granules and spindle-shaped food vacuoles containing parallel arranged bacteria. Undulating membranes short, forming an acute angle. 1 short frontoventral row.



Figs 56–60 *Terricirri matsusakai* from life (Figs 56–58) and after protargol impregnation (Figs 59, 60). **56–58** Ventral, lateral, and dorsal view. Figure 58 shows the arrangement of the dark-green, spherical subpellicular granules. **59, 60** Infraciliature in ventral and dorsal view.

TYPE-SPECIES .*Terricirra viridis* (Foissner, 1982) nov. comb. (basionym: *Perisincirra viridis* Foissner, 1982).

COMPARISON WITH RELATED GENERA. The conspicuous combination of the characters—green to blue subpellicular granules, spindle-shaped food vacuoles, and the markedly differently orientated short undulating membranes—is unique within the hypotrichs. It separates *Terricirra* distinctly from the genera *Hemisincirra* Hemberger, 1985 and *Lamtostyla* Buitkamp, 1977*a* which have a very similar infraciliature (Berger & Foissner, 1988*a*). The same type of food vacuoles occurs in the colpodid ciliate *Parabryophrya penardi* (Kahl, 1931) Foissner, 1985.

The other two species which have to be included in the new genus are *Terricirra matsusakai* (see below) and *T. livida* (Berger & Foissner, 1987) nov. comb. (basionym: *Hemisincirra livida* Berger & Foissner, 1987). Recently, two further species of this genus were found in soils of Denmark and Australia (Foissner, unpublished). This supports the establishment of *Terricirra* which is very probably restricted to soil (Foissner, 1987*c*).

Terricirra matsusakai nov. spec.

DIAGNOSIS. *In vivo c.* 125–135 × 27–30 µm. Subpellicular granules dark green, spherical, *c.* 1 µm in diameter. 18 adoral membranelles on average, 4 macronuclear segments, 4 dorsal kineties.

TYPE LOCATION. Soil of a rice field of Kyokushi, Kumamoto Prefecture, Japan.

DEDICATION. This species is named in honour of Dr Tadao Matsusaka, University of Kumamoto, who collected the soil samples from Japan.

DESCRIPTION (Figs 56–60, Tables 1, 9). Body margins parallel, in the area of the adoral zone of membranelles distinctly converging, both ends rounded. Very flexible, slightly contractile, 1.5–2 : 1 flattened. Macronuclear segments *in vivo c.* 15 × 11 µm, arranged in the median of the cell or slightly left of it. Contractile vacuole in the middle of the cell, during diastole with distinct channels. About 6 loose rows of subpellicular granules on the ventral and dorsal surface, respectively. Cytoplasm colourless, with many *c.* 7–9 µm long food vacuoles, 1–2 µm large fat globules, and cytoplasmatic crystals.

Adoral zone of membranelles c. 19% of body length. Buccal area flat and narrow, the posterior part of the buccal area covered by a hyaline cytoplasmatic roof. Marginal and transverse cirri *in vivo c.* 10 µm and 15 µm long, respectively. The latter one arranged in a short, rather oblique row. Dorsal kinety 1 slightly shortened at both ends, kineties 2 and 3 of body length, and kinety 4 terminates in about the middle of the cell. Dorsal cilia *in vivo c.* 2 µm long. Caudal cirri absent.

The morphogenesis commences with the apokinetal formation of the oral primordium in about the middle of the cell.

COMPARISON WITH RELATED SPECIES. *Terricirra matsusakai* differs from the rather similar *Hemisincirra quadrinucleata* Hemberger, 1985, which also has the same type of undulating membranes, in that it has more dorsal kineties, no interruption in the adoral zone of membranelles, and a more posteriorly located contractile vacuole. Since Hemberger (1985) gives no

Table 10 Biometrical characterization of *Oxytricha islandica* (upper line), *Oxytricha lanceolata* (middle line), and *Oxytricha longigranulosa* (lower line)

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	93.3	96.5	12.1	3.839	13.0	72.0	115.0	10
	94.5	96.0	12.2	3.842	12.9	70.0	108.0	10
	87.6	91.0	8.5	2.344	9.6	72.0	98.0	13
Body, width	30.7	31.0	3.6	1.146	11.8	25.0	35.0	10
	34.2	34.5	3.4	1.083	10.0	29.0	42.0	10
	31.9	32.0	3.1	0.866	9.8	27.0	38.0	13
Adoral membranelles, number	26.7	27.0	2.3	0.715	8.5	21.0	29.0	10
	27.6	28.0	0.8	0.267	3.1	26.0	29.0	10
	26.5	27.0	1.1	0.291	4.0	24.0	28.0	13
Adoral zone of membranelles, length	29.1	30.0	2.7	0.849	9.2	22.0	31.0	10
	30.1	31.5	3.5	1.100	11.6	24.0	34.0	10
	28.1	28.0	1.3	0.366	4.7	25.0	30.0	13
Macronuclear segments, number	4.2	4.0	0.6	0.200	15.1	4.0	6.0	10
	2.0	2.0	0	0	0	2.0	2.0	10
	2.0	2.0	0	0	0	2.0	2.0	13
Macronuclear segments, distance between	–	–	–	–	–	–	–	0
	8.5	10.0	2.7	0.860	32.0	3.0	11.0	10
	11.7	12.0	2.8	0.763	23.5	7.0	16.0	13
Posterior macronuclear segment, length	13.1	13.0	2.1	0.657	15.9	9.0	17.0	10
	13.9	14.5	1.6	0.504	11.5	10.0	15.0	10
	14.8	14.0	1.8	0.496	12.1	12.0	17.0	13
Posterior macronuclear segment, width	7.4	7.0	0.2	0.163	7.0	7.0	8.0	10
	6.9	7.0	0.9	0.277	12.7	5.0	8.0	10
	7.6	7.0	0.8	0.213	10.1	7.0	9.0	13
Micronuclei, number	1.8	2.0	0.4	0.133	23.4	1.0	2.0	10
	1.8	2.0	0.6	0.200	35.1	1.0	3.0	10
	1.2	1.0	0.4	0.104	32.5	1.0	2.0	13
Posterior micronucleus, length	3.1	3.0	0.2	0.066	6.8	3.0	3.5	10
	2.8	2.8	0.1	0.020	2.2	2.8	3.0	10
	2.7	2.8	0.4	0.123	16.2	2.0	3.5	13
Posterior micronucleus, width	3.1	3.0	0.2	0.066	6.8	3.0	3.5	10
	2.6	2.6	0.2	0.050	6.0	2.4	2.8	10
	2.4	2.5	0.4	0.104	15.7	2.0	3.0	13
Left marginal row, number of cirri	26.2	26.0	2.9	0.928	11.2	22.0	32.0	10
	31.7	32.0	3.6	1.136	11.3	25.0	36.0	10
	22.9	23.0	1.4	0.390	6.2	21.0	25.0	13
Right marginal row, number of cirri	25.6	26.5	2.2	0.686	8.5	21.0	28.0	10
	28.5	28.0	1.9	0.601	6.7	26.0	32.0	10
	25.9	26.0	1.6	0.436	6.1	23.0	28.0	13
Frontal cirri, number[1]	3.0	3.0	0	0	0	3.0	3.0	10
Buccal cirri, number[1]	1.0	1.0	0	0	0	1.0	1.0	10
Frontoventral cirri, number[1]	4.0	4.0	0	0	0	4.0	4.0	10
Postoral ventral cirri, number[1]	3.0	3.0	0	0	0	3.0	3.0	10
Ventral cirri near the transverse cirri, number[1]	2.0	2.0	0	0	0	2.0	2.0	10
Transverse cirri, number[1]	5.0	5.0	0	0	0	5.0	5.0	10
Caudal cirri, number[1]	3.0	3.0	0	0	0	3.0	3.0	10
Dorsal kineties, number	4.1	4.0	0.3	0.100	7.7	4.0	5.0	10
	4.0	4.0	0	0	0	4.0	4.0	10
	6.0	6.0	0	0	0	6.0	6.0	13

[1] These values are valid for *O. lanceolata* (n = 10) and *O. longigranulosa* (n = 13) too.

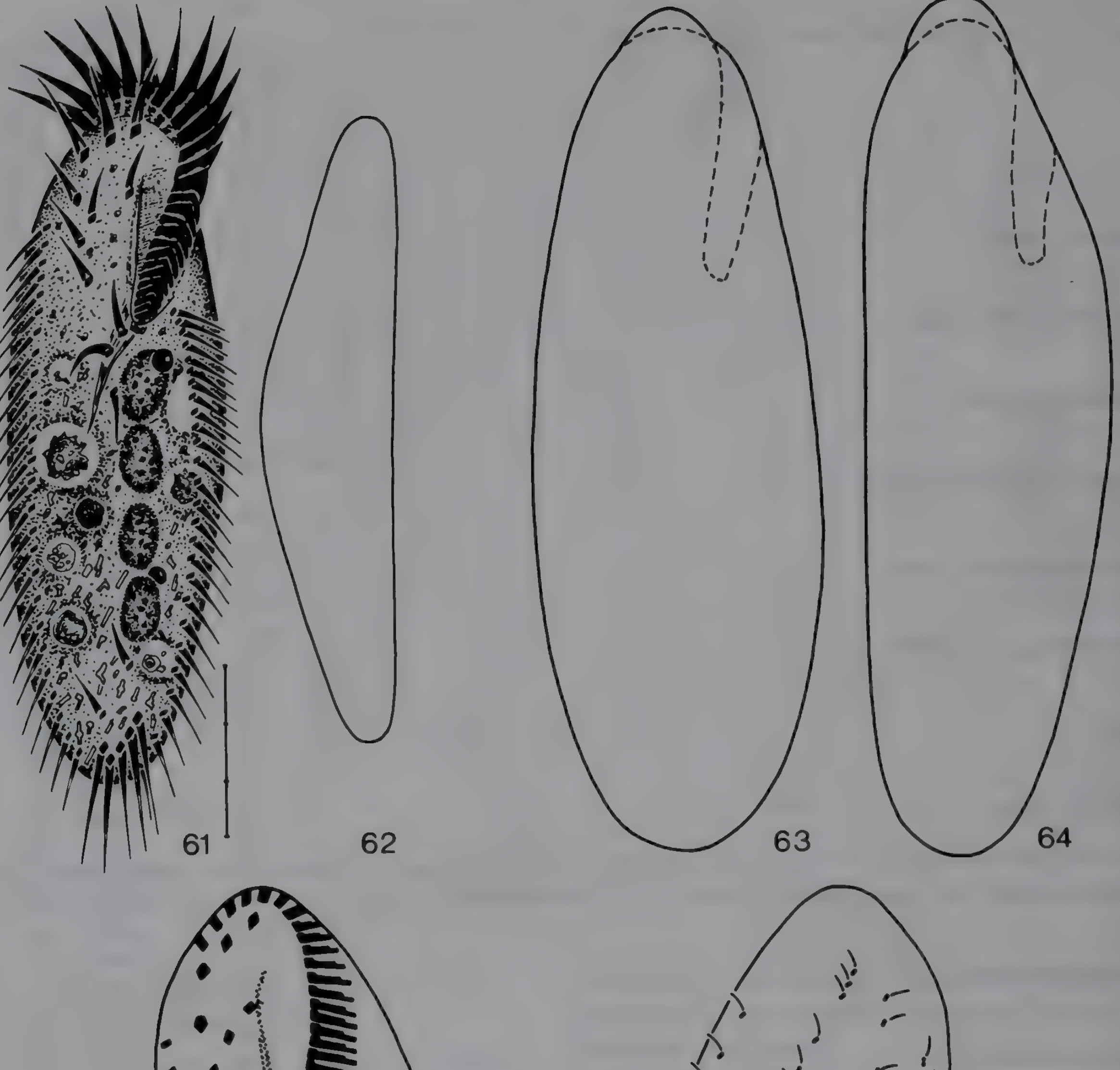
information about the food vacuoles and the subpellicular granules, *H. quadrinucleata* is not transferred to the new genus. *Terricirra matsusakai* can be distinguished from *T. viridis* and *T. livida* by the body shape and the number of macronuclear segments, dorsal kineties, transverse cirri, and cirri in the frontoventral row.

Oxytricha islandica nov. spec.

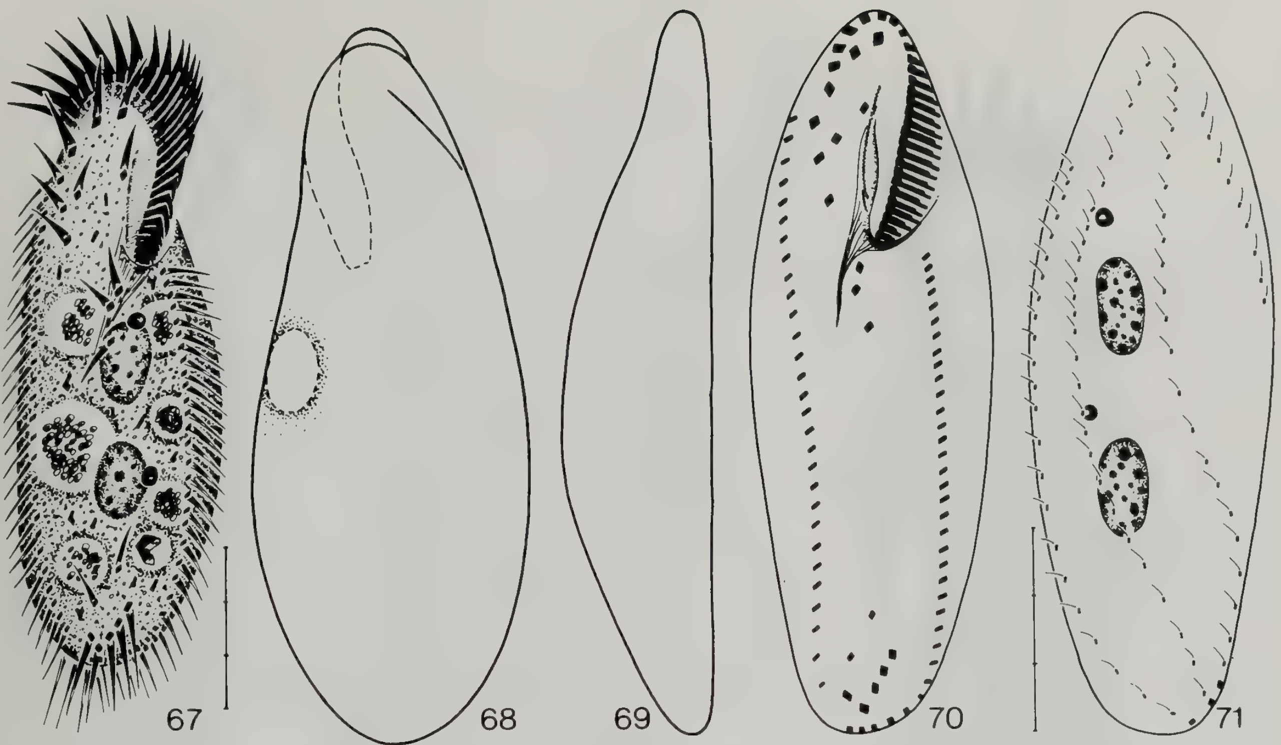
DIAGNOSIS. *In vivo* 100–140 × 35–45 µm. Usually 4 macronuclear segments. About 27 adoral membranelles, *c.* 26 left and 26 right marginal cirri. 4 dorsal kineties.

TYPE LOCATION. Pasture with moss and *Deschámpsia caespitósa* on the peninsula Vatnsney 'Hvitserkur', Iceland.

DESCRIPTION (Figs 61–66, Tables 1, 10). Body ellipsoid, left margin sometimes straight, right one distinctly convex, posteriorly distinctly converging. Both ends rounded. About 2 : 1 flattened. Very flexible, slightly contractile. Macronuclear segments *in vivo c.* 13 × 10 µm, arranged in a line almost in the median of the cell or slightly left of it. Micronuclei *in vivo* about 4 µm in diameter. Contractile vacuole somewhat above the middle of the cell, during diastole without distinct channels. Subpellicular granules absent. Cytoplasm colourless, posteriorly



Figs 61–66 *Oxytricha islandica* from life (Figs 61–64) and after protargol impregnation (Figs 65, 66). **61–64** Ventral and lateral views. **65, 66** Infraciliature in ventral and dorsal view.



Figs 67–71 *Oxytricha lanceolata* from life (Figs 67–69) and after protargol impregnation (Figs 70, 71). **67–69** Ventral, dorsal, and lateral view. **70, 71** Infraciliature in ventral and dorsal view.

filled with many cytoplasmic crystals and numerous food vacuoles (*c.* 10 µm in diameter) containing cysts of amoebae and unidentified material. Rapid movement.

Adoral zone of membranelles about 31% of body length. Bases of the largest membranelles *in vivo c.* 7 µm wide. Buccal area flat, undulating membranes nearly straight. Buccal cirrus inserted at about the level of the posterior end of the endoral membrane. Typical *Oxytricha* cirral pattern. Frontal, marginal, and transverse cirri *in vivo c.* 15 µm, 14 µm, and 22 µm long, respectively. Dorsal kineties 1–3 distinctly bent, kinety 1 slightly shortened anteriorly, kinety 4 terminates roughly in the middle of the cell. Dorsal cilia *in vivo c.* 3 µm long. Caudal cirri on kineties 1–3.

COMPARISON WITH RELATED SPECIES. *Oxytricha islandica* differs from the other *Oxytricha* species in that it has 4 macronuclear segments (compare Kahl, 1932; Stiller, 1974). It can be distinguished from other quadrinucleate members of the family by the habitat, the body shape, the body size, and the ventral and dorsal infraciliature (Quennerstedt, 1987; Kahl, 1932, 1935; Gelei & Szabados, 1950; Dragesco, 1966; Dragesco & Njine, 1971; Foissner, 1980, 1982, 1984; Berger & Foissner, 1987).

Oxytricha lanceolata Shibuya, 1930

DISCUSSION AND ADDITIONAL OBSERVATIONS (Figs 67–71, Tables 1, 10). It is widely assumed that oxytrichids are rather variable. This is not in accordance with our experience. To document this once more, we shortly describe here a further population of *O. lanceolata* from Madeira. This *in vivo* about 110 × 50 µm large population agrees very well in all characters (e.g. absence of subpellicular granules, number of adoral membranelles) with the Austrian population described by Berger & Foissner (1987).

Cytoplasm made opaque by small (< 1 µm), fat globules. Food vacuoles *c.* 8–16 µm, with globular green algae, zooflagellates, and crystaline content. Distinct dorsal furrow right anteriorly. Undulating membranes only inconspicuously bent, nearly superimposed. Caudal cirri motile.

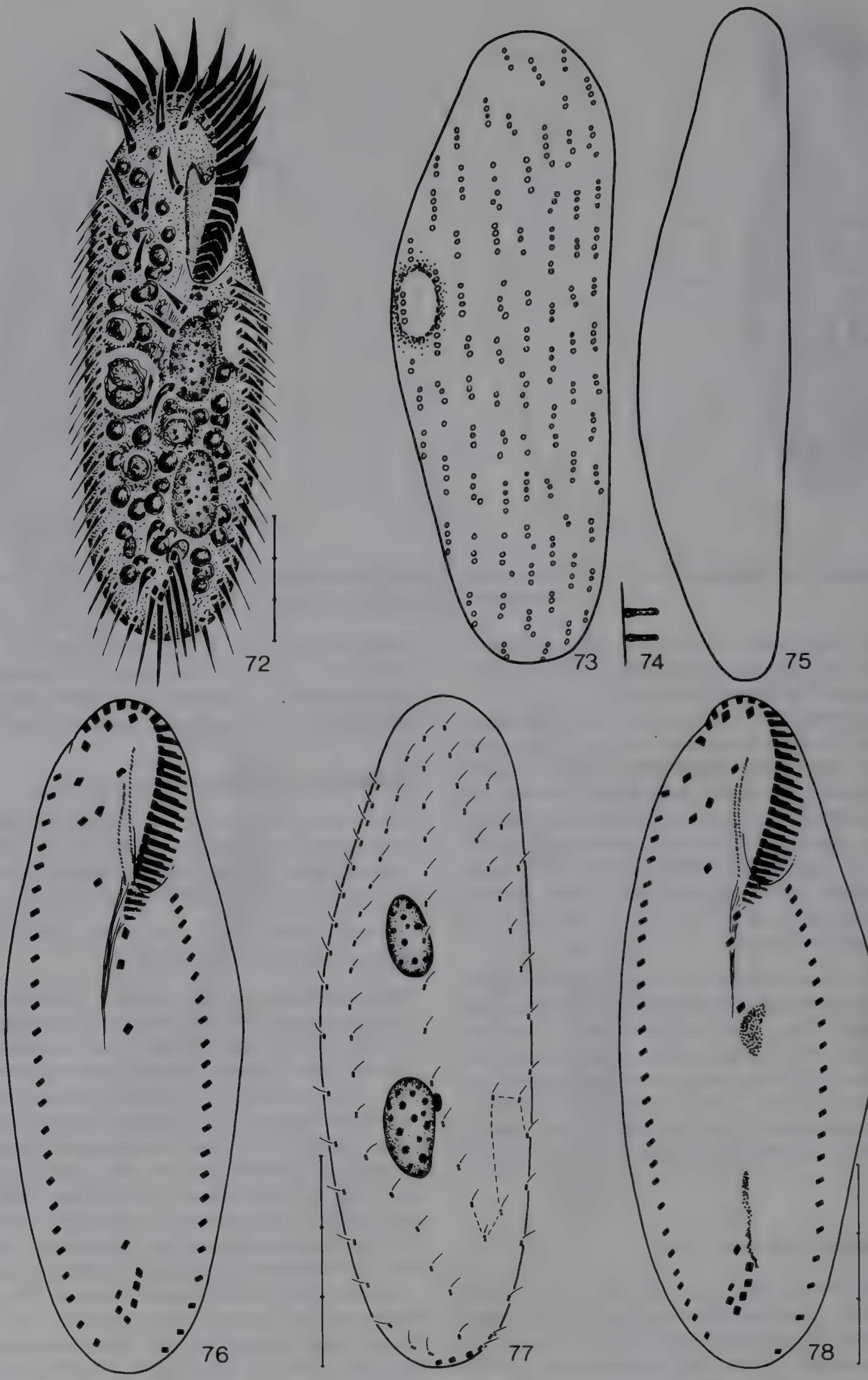
Oxytricha longigranulosa nov. spec.

DIAGNOSIS. *In vivo* about 135 × 55 µm. Subpellicular granules (extrusomes) colourless, rod-shaped, c. 2–3 µm long, arranged in short rows. 26 adoral membranelles, 25 right, and 23 left marginal cirri on average. 6 dorsal kineties.

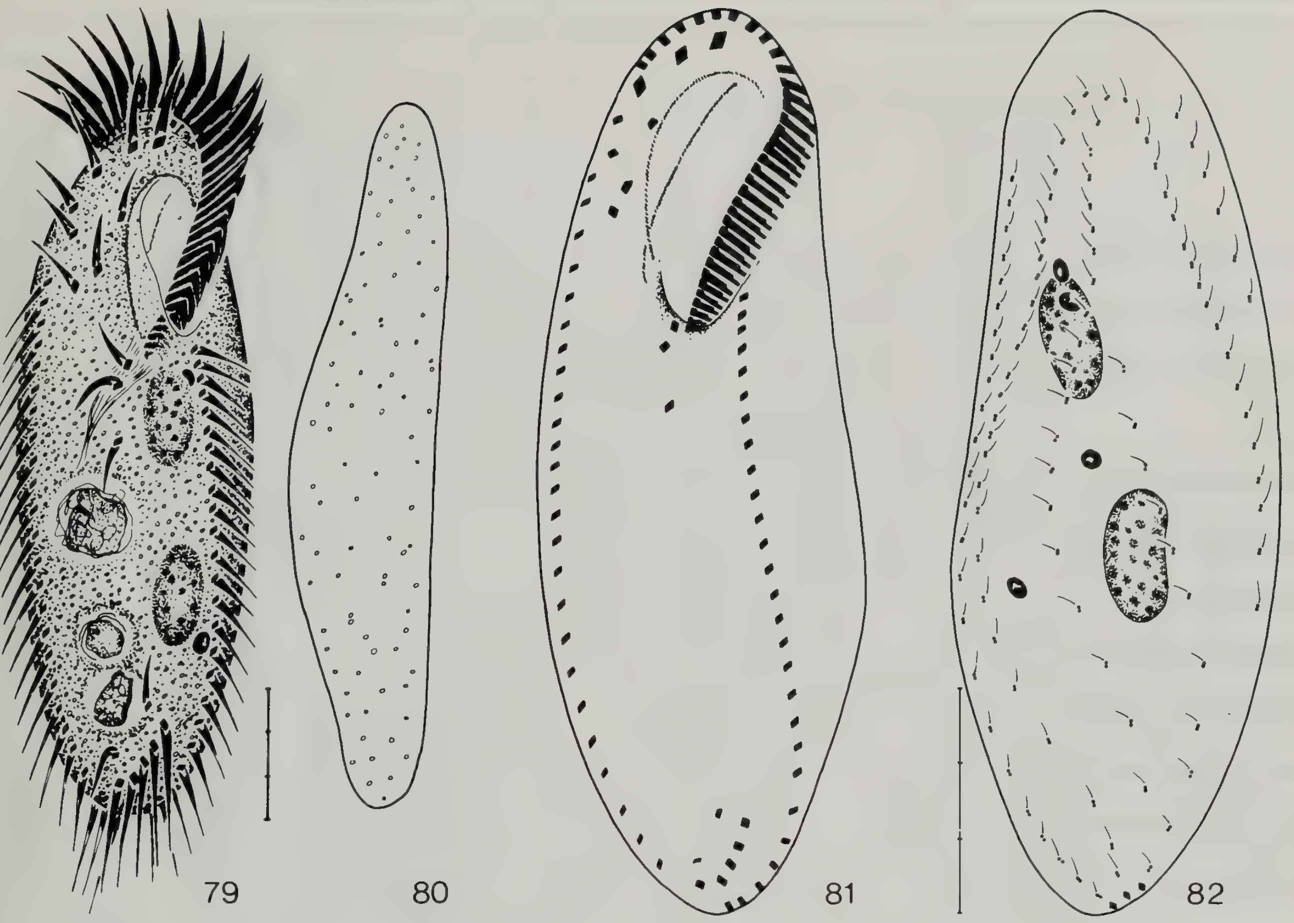
TYPE LOCATION. Soil from Mt Kura-Take, Amakusa, Kumamoto Prefecture, Japan.

DESCRIPTION (Figs 72–78, Tables 1, 10). Body ellipsoid, right margin straight, left one distinctly bent out at the level of the contractile vacuole. Both ends rounded. About 2 : 1 flattened, very flexible. Macronuclear segments lying slightly left of the median. Contractile vacuole slightly above the middle of the cell, during diastole without channels. Extrusomes anteriorly with an inconspicuous knob, stain red with methylgreen-pyronin, but were not ejected. Cytoplasm colourless, with *c.* 5 µm large fat globules and many food vacuoles containing fungal spores, zooflagellates, and ciliates. Hence, the specimens appear slightly brownish at low magnification. Gliding movement, sometimes nearly jumping.

Adoral zone of membranelles about 32% of body length. Bases of the largest membranelles in vivo *c.* 7 µm wide. Buccal area flat and narrow, undulating membranes nearly straight. Bases of all cirri nearly of the same size. Typical *Oxytricha* cirral pattern. Marginal and transverse cirri *in vivo c.* 15 µm and 20 µm long, respectively. Dorsal kineties 1 and 2 nearly of body length, kinety 3 with a bend at the posterior end and kinety 4 distinctly bent to the left anteriorly so that the connexion of these 2 kineties is still recognizable. Kinety 5 half of body length, kinety 6 consists of about 4 basal body



Figs 72–78 *Oxytricha longigranulosa* from life (Figs 72–75) and after protargol impregnation (Figs 76–78). **72, 73** Ventral and dorsal view. Figure 73 shows the arrangement of the 2–3 µm long, colourless extrusomes. **74** Extrusomes in lateral view. **75** Lateral view. **76, 77** Infraciliature in ventral and dorsal view. In Figure 77 the posterior end of dorsal kinety 3 and the anterior end of dorsal kinety 4 are connected by a dotted line. **78** Early morphogenetic stage in ventral view.



Figs 79–82 *Steinia muscorum* from life (Figs 79, 80) and after protargol impregnation (Figs 81, 82). **79** Ventral view. **80** Lateral view. Red granules (c. 1 µm) close beneath the pellicle and in the ctyoplasm. **81, 82** Infraciliature in ventral and dorsal view.

pairs only. Dorsal cilia *in vivo c.* 3 µm long. Caudal cirri on kineties 1, 2, and 4.

COMPARISON WITH RELATED SPECIES. So far only 2 *Oxytricha* species with subpellicular granules have been described: *O. granulifera* Foissner & Adam, 1983 and *O. rubripuncta* Berger & Foissner, 1987. *Oxytricha longigranulosa* differs from these species in the shape, size, colour, and arrangement of the subpellicular granules and the number of dorsal kineties and adoral membranelles. The beginning of the morphogenesis is rather similar to that of *O. granulifera* (Foissner & Adam, 1983).

Steinia muscorum Kahl, 1932

DISCUSSION AND ADDITIONAL OBSERVATIONS (Figs 79–82, Tables 1, 11). Since 1982 we have observed many populations of this species and found them to be usually a little wider than that figured in Foissner (1982). Thus, we show the morphology of such a population. The biometrical data agree well with that of Buitkamp (1977*b*) and Foissner (1982).

In vivo 140–160 × 55–60 µm, about 2 : 1 flattened. Buccal area large, partly covered by a hyaline projection. Feeds on fungal spores, zooflagellates, testaceans (*Schoenbornia* sp.), and ciliates (*Odontochlamys* sp., *Opercularia* sp., *Gonostomum* sp.). Very rarely a seventh dorsal kinety, which consists of 2–4 basal body pairs only.

Urosoma octonucleata nov. spec.

DIAGNOSIS. *In vivo* about 140–180 × 25–40 µm, vermiform. 8 macronuclear segments and 25 adoral membranelles on average. 3–4 transverse cirri (including the ventral cirri nearby).

TYPE LOCATION: Soil in Garajan Kap, Madeira, Portugal.

DESCRIPTION (Figs 83–88, Tables 1, 11). Anterior end rounded, posterior one tapered and usually bent to the right. About 2 : 1 flattened, very flexible. Macronuclear segments *in vivo* 7 × 5 µm, arranged in a line slightly left of the median. Micronuclei in *vivo c.* 4 µm in diameter. Contractile vacuole distinctly above the middle of the cell, during diastole with 2 channels. Close beneath the pellicle numerous colourless, 2 µm large ellipsoid structures (mitochondria ?). Subpellicular granules absent. Cytoplasm colourless, with numerous 1 µm large, colourless granules and some *c.* 7 µm large food vacuoles containing bacteria. In the posterior part many cytoplasmatic crystals.

Adoral zone of membranelles about 23% of body length, the distal 4 membranelles slightly separated from the proximal, nearly perpendicular arranged part. Bases of the largest membranelles *in vivo c.* 5 µm wide. Buccal area very flat, undulating membranes nearly straight. Buccal cirrus inserted at the anterior end of the paroral membrane. Frontal cirri only slightly enlarged, *in vivo c.* 14 µm long. Cirrus behind the right frontal cirrus slightly enlarged, situated anteriorly to the remaining frontoventral cirri of the frontal area. Postoral ventral cirri arranged in a line. 2 transverse cirri slightly enlarged. Marginal cirri *in vivo c.* 10 µm long, posteriorly the distance among the cirri is distinctly wider than anteriorly. Dorsal cilia about 3 µm long. Dorsal kinety 1 and 4 anteriorly and posteriorly shortened, respectively. Caudal cirri on kineties 1–3.

Table 11 Biometrical characterization of *Steinia muscorum* (upper line) and *Ursoma octonucleata* (lower line)

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	129.4	126.0	14.7	3.123	11.3	105.0	155.0	22
	141.2	145.0	13.5	4.072	9.6	105.0	155.0	11
Body, width	47.7	48.5	5.3	1.135	11.2	36.0	56.0	22
	25.8	25.0	1.9	0.585	7.5	22.0	28.0	11
Adoral membranelles, number	34.8	36.0	3.9	0.823	11.1	24.0	40.0	22
	25.1	25.0	0.7	0.211	2.8	24.0	26.0	11
Adoral zone of membranelles, length	42.1	42.0	4.9	1.043	11.6	32.0	52.0	22
	33.2	34.0	2.0	0.600	6.0	29.0	36.0	11
Macronuclear segments, number	2.0	2.0	0	0	0	2.0	2.0	22
	7.6	8.0	0.8	0.247	10.9	6.0	8.0	11
Distance 1[1]	16.0	15.5	4.0	0.846	24.8	11.0	24.0	22
	56.0	56.0	4.4	1.335	7.9	48.0	65.0	11
Posterior macronuclear segment, length	20.5	21.0	2.8	0.606	13.9	14.0	25.0	22
	7.6	8.0	0.5	0.157	6.9	7.0	8.0	11
Posterior macronuclear segment, width	9.5	10.0	1.7	0.371	18.4	6.0	14.0	22
	5.0	5.0	0.9	0.270	17.9	4.0	6.0	11
Micronuclei, number	2.5	2.0	0.6	0.127	23.9	2.0	4.0	22
	2.1	2.0	0.3	0.091	14.4	2.0	3.0	11
Posterior micronucleus, length	3.9	4.0	0.4	0.091	11.1	3.0	4.0	22
	3.0	3.0	0.2	0.055	6.0	2.8	3.5	11
Posterior micronucleus, width	2.8	2.8	0.2	0.035	5.8	2.5	3.0	22
	2.0	2.0	0.2	0.059	10.1	1.5	2.2	11
Left marginal row, number of cirri	24.7	25.5	2.6	0.552	10.5	20.0	29.0	22
	31.1	32.0	1.7	0.513	5.5	28.0	34.0	11
Right marginal row, number of cirri	23.0	23.5	1.7	0.369	7.5	20.0	25.0	22
	37.3	38.0	1.8	0.541	4.8	35.0	40.0	11
Frontal cirri, number	3.0	3.0	0	0	0	3.0	3.0	22
	3.0	3.0	0	0	0	3.0	3.0	11
Buccal cirri, number	1.0	1.0	0	0	0	1.0	1.0	22
	1.0	1.0	0	0	0	1.0	1.0	11
Frontoventral cirri, number	4.0	4.0	0	0	0	4.0	4.0	22
	4.0	4.0	0	0	0	4.0	4.0	11
Postoral ventral cirri, number	3.0	3.0	0	0	0	3.0	3.0	22
	2.9	3.0	0.3	0.091	10.4	2.0	3.0	11
Ventral cirri near the transverse cirri, number	2.0	2.0	0	0	0	2.0	2.0	22
	–	–	–	–	–	–	–	0
Transverse cirri, number[2]	5.0	5.0	0	0	0	5.0	5.0	22
	3.5	3.0	0.5	0.157	15.1	3.0	4.0	11
Caudal cirri, number	3.0	3.0	0	0	0	3.0	3.0	22
	3.1	3.0	0.3	0.091	9.6	3.0	4.0	11
Dorsal kineties, number	6.1	6.0	0.3	0.063	4.8	6.0	7.0	22
	4.0	4.0	0	0	0	4.0	4.0	11
Distance 2[1]	4.1	4.0	1.1	0.227	26.0	3.0	7.0	22
	14.2	15.0	2.4	0.711	16.6	10.0	18.0	11

[1] Distance 1, distance between the macronuclear segments (*S. muscorum*) and length of the macronucleus figure (*U. octonucleata*), respectively. Distance 2, distance between the posterior transverse cirrus and the posterior end of the cell.
[2] In *U. octonucleata* adjacent ventral cirri are included.

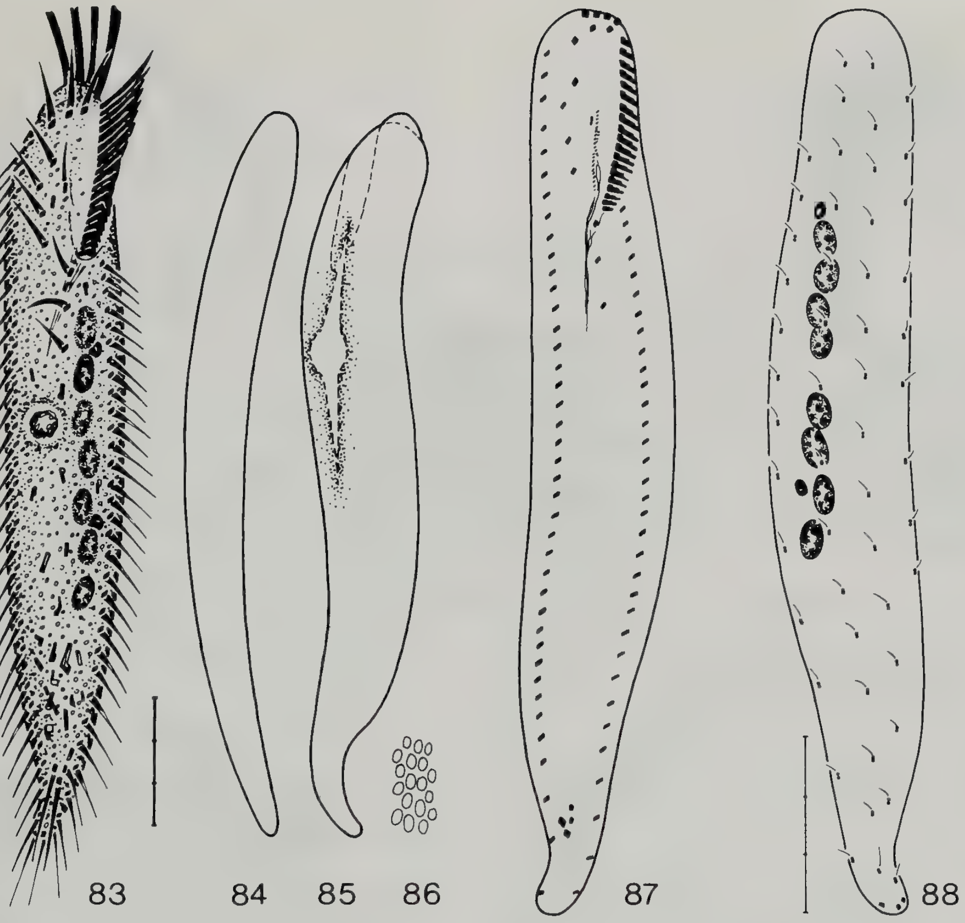
COMPARISON WITH RELATED SPECIES. The arrangement of the frontoventral cirri in the frontal area, the slightly enlargement of the cirrus III/2, and the body shape require the classification in the genus *Urosoma* Kowalewski, 1882 (Foissner, 1987*a*; Berger & Foissner, 1988*c*).

Urosoma octonucleata can be distinguished from the other congeneric species by the higher number of macronuclear segments and the lower number of transverse cirri (Kahl, 1932; Dragesco, 1972; Foissner, 1982, 1984, 1987*a*; Dragesco & Dragesco-Kerneis, 1986; Berger & Foissner, 1987). *In vivo, U. octonucleata* can be easily confused with *Hemisincirra polynucleata* Foissner, 1984, because the body shape, the nuclear apparatus, and the arrangement of the mitochondria close beneath the pellicle are very similar (Foissner, 1984, Abb. 63). Additionally, the infraciliature of the frontal area and the dorsal surface and many biometrical characters are largely identical. However, the species can be clearly separated by the number of postoral ventral cirri (*U. octonucleata* 3; *H. polynucleata* 1) and the number and the position of the transverse cirri including the adjacent ventral cirri (3–4, distinctly subterminal; 2, terminal).

Euplotes corsica nov. spec.

DIAGNOSIS. *In vivo* about 40 × 20 µm, oval, about hemispherical in cross-section. 10 frontoventral, 5 transverse, and 3–4 caudal cirri, 7–8 dorsolateral kineties. 22 adoral membranelles on average. Dorsal argyrome of double-eurystomus type.

TYPE LOCATION. Soil of a saline pool at the Etang d'Urbino, Corsica, France.

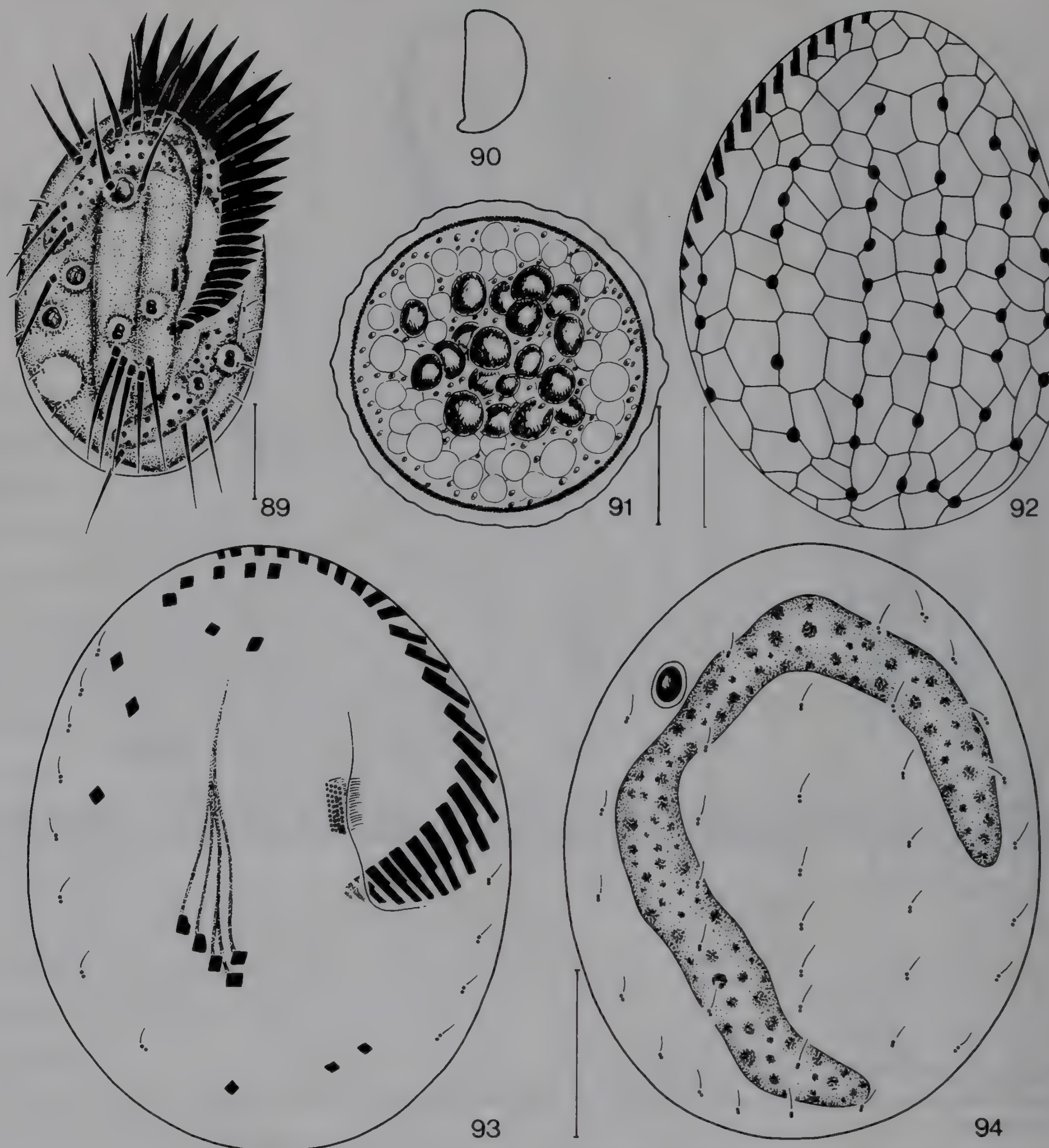


Figs 83–88 *Urosoma octonucleata* from life (Figs 83–86) and after protargol impregnation (Figs 87, 88). **83–85** Ventral, lateral, and dorsal view. **86** Colourless, c. 2 µm large structures (mitochondria?) close beneath the pellicle. **87, 88** Infraciliature in ventral and dorsal view.

Table 12 Biometrical characterization of *Euplotes corsica*

Character	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	35.5	35.0	3.8	0.833	10.8	29.0	42.0	21
Body, width	27.6	28.0	2.6	0.567	9.4	22.0	32.0	21
Adoral membranelles, number	22.2	22.0	1.2	0.264	5.4	20.0	25.0	21
Adoral zone of membranelles, length	22.0	21.0	2.1	0.447	9.3	17.0	25.0	21
Paroral membrane, length	3.1	3.0	0.4	0.076	11.5	2.0	4.0	21
Macronucleus, length[1]	29.9	31.0	3.9	0.840	12.9	20.0	36.0	21
Macronucleus, width	4.7	4.0	0.9	0.197	19.2	4.0	6.0	21
Micronucleus, length	3.0	3.0	0.1	0.024	3.6	3.0	3.5	21
Micronucleus, width	2.2	2.0	0.3	0.055	11.7	1.8	2.5	21
Distance 1[2]	8.6	8.0	2.2	0.471	25.2	6.0	12.0	21
Frontal cirri, number	3.0	3.0	0	0	0	3.0	3.0	21
Distance 2[3]	4.0	4.0	0	0	0	4.0	4.0	21
Ventral cirri, number	7.0	7.0	0	0	0	7.0	7.0	21
Transverse cirri, number	5.0	5.0	0	0	0	5.0	5.0	21
Caudal cirri, number	3.2	3.0	0.4	0.087	12.6	3.0	4.0	21
Dorsolateral kineties, number	7.5	7.0	0.5	0.112	6.8	7.0	8.0	21
Dorolateral kinety 5, number of basal body pairs	7.5	8.0	0.9	0.203	12.3	6.0	9.0	21
Cyst, large diameter[4]	26.7	27.5	2.5	0.710	9.2	22.0	31.0	12
Cyst, small diameter[4]	25.1	25.0	2.4	0.679	9.4	21.0	28.0	12

[1] Distance between the anteriormost and posteriormost point of the macronucleus.
[2] Distance between the anterior end of the cell and the anterior end of the micronucleus.
[3] Distance between the right edge of the right and the left edge of the left frontal cirrus.
[4] From life culture material.



Figs 89–94 *Euplotes corsica* from life (Figs 89–91), after wet silver impregnation (Fig. 92), and after protargol impregnation (Figs 93, 94). **89, 90** Ventral and lateral view. **91** Cyst. **92** Dorsal argyrome. **93, 94** Infraciliature in ventral and dorsal view.

DESCRIPTION (Figs 89–94, Tables 1, 12). Posterior third of the cell with a hyaline edge, especially on the right side. Ventral surface with 3 median ridges. Dorsal surface only slightly ridged, protrudes beyond the ventral surface posteriorly. About 2 : 1 flattened. Contractile vacuole at about the level of the transverse cirri, conspicuously near the body margin. Cytoplasm colourless, filled with many *c.* 5 µm large food vacuoles and some vacuoles containing 4 µm large, dumbbell-shaped crystals. Rapid movement.

Adoral zone of membranelles about 62% of body length. Cirri fine, transverse cirri *in vivo c.* 20 µm long, do not protrude beyond the posterior margin.

Cyst slightly elliptical, wall about 1.4 µm thick. Outer layer yellowish, fine irregularly wrinkled. Cytoplasm densely filled with bright vacuoles (3–4 µm in diameter) and 3–5 µm large clod-like inclusions.

COMPARISON WITH RELATED SPECIES. *Euplotes corsica* is very probably conspecific with the *E. alatus* Kahl, 1932 of Borror (1968) from a tidal marsh pond. It differs from the original description of *E. alatus* and the population of Gelei (1938) in the shape and size of the body and the number of dorsolateral kineties, respectively. It can be distinguished from the other species of the 'double-eurystomus' type listed in Curds (1975) in the body size and the nearly hemispherical body shape to name but two characters. The rather similar limnetic species *E. palustris* Ten Hagen, 1980, which is 45–55 µm long, has a dorsal argyrome of the 'double-patella' type.

ACKNOWLEDGEMENTS The authors wish to thank Dr Tadao Matsusaka (Kumamoto University, Japan), Dr Wolfgang Vetters and Dr Norbert Winding, Mr Bruno Ganner, and Mr Wolfgang Petz (University of Salzburg) for providing soil samples from Japan, Iceland, Corsica, and Madeira, respectively. The photographic assistance of Ms Karin Bernatzky and Mr Rudolf Hametner is greatly acknowledged. The study was supported by the 'Fonds zur Förderung der wissenschaftlichen Forschung, Projekt Nr. P 5889'.

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Bull. Br. Mus. nat. Hist (Zool.) **55**(1): 47–96 Issued 25 May 1989

Polyclad turbellarians recorded from African waters

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Synopsis. This work lists species of polyclad turbellarians reported from African waters since 1826. Ninety-seven species have hitherto been recorded, but only 16 of them were noted during the nineteenth century. As the result of the present writer's studies, the number is now increased to 142, which includes 6 new genera and 29 new species. The new material came from South Africa, Inhaca Island and the Comoro Islands in the Mozambique Channel, the Red Sea and the Gulf of Aqaba, Morocco and West Africa. Included in this work are differential keys to families, genera and species, as well as diagnoses of species of the leptoplanid genera *Stylochoplana* and *Notoplana*. The problem of speciation within the genus *Pseudoceros* is discussed.

INTRODUCTION

Polyclad turbellarians occurring along the African coasts have been little explored. Known studies have provided information on specimens from the Red Sea, South Africa and isolated localities on the coasts of Angola, Senegal, Ghana, Sierra Leone, Mauritania and Morocco. Unfortunately, the descriptions of several species published during the nineteenth century are unrecognizable, in fact, only 6 of the 15 or so species reported are now recognizable with any degree of certainty.

Material available to the writer was obtained from Inhaca I., Mozambique, by Dr Vivien Gabie, formerly of the Witwatersrand University, Johannesburg, from the Comoro

Is in the northern region of the Mozambique Channel by Dr P. Bouchet of the Museum National d'Histoire Naturelle, Paris, from South Africa by Professor John H. Day and students of Cape Town University during ecological surveys along the South African coast, from Morocco by Dr Ghazi Bitar formerly of the Rabat Institute and from collectors who have from time to time sent specimens to the British Museum (Natural History) for identification. Dr Gabie's material also includes a number of water-coloured paintings of living worms and that of Dr Bouchet some colour-transparencies again of living specimens.

It should be mentioned that the Inhaca collection was originally submitted to the late Dr Libbie H. Hyman in 1959 for examination. After recognizing *Stylochoplana inquilina* and *Pseudoceros bedfordi*, Miss Hyman appears to have felt unable, because of ill-health, to continue with her study and returned the collection to Dr Gabie in 1967 with the suggestion that the present writer might be willing to undertake its examination. All specimens have been studied, firstly, as whole mounts cleared in methyl salicylate and, secondly, in some instances, as longitudinal serial sections of the copulatory organs. The specimens, water-coloured paintings and the colour-transparencies have been incorporated into the helminthological collections of the British Museum (Natural History). The registration numbers of type-material are given below.

In view of an entirely new classification of the Polycladida recently proposed by Faubel (1983, 1984) it needs to be mentioned that the classification here used is that erected by Lang (1884) and later modified by Bock (1913), Bresslau (1928–30), Hyman (1951), Marcus and Marcus (1968) and Prudhoe (1985). Faubel's classification is based on the presence or absence of a prostatic vesicle and, when present, its structure and its relationship with the ejaculatory duct. In the present writer's experience, when the male phase of the worm reaches its peak a prostate is invariably present, in one form or other, varying from a muscular vesicle to a mere gathering of prostate gland-cells investing or lining a portion of the ejaculatory duct (*sensu lato*). The male copulatory complex often undergoes much structural change during its development, so that a complex in a young, but not sexually functional, adult may appear different in the fully functional complex.

Unfortunately, Dr Faubel's work contains a number of inaccuracies among his family and generic definitions. He also seems to have been unaware of the existence of the International Code of Zoological Nomenclature, which, if applied, would assign several of his new generic names to synonymy.

Finally, the writer is most grateful to Mr David Cooper of the histology section of the British Museum (Natural History) for preparing excellent serial sections of several worms included in this investigation.

SYSTEMATIC SECTION

Order **POLYCLADIDA** Lang, 1884, emend. Gamble, 1893

Key to suborders of Polycladida recorded from African waters

1 Usually with ventral sucker, adhesive pad or depression posterior to female genital pore; tentacles, when present, antero-marginal (except *Opisthogenia*) .... ***COTYLEA***

2 Without ventral adhesive structure posterior to female pore; tentacles, when present, nuchal ... ***ACOTYLEA***

Suborder **ACOTYLEA** Lang, 1884

Diagnostic features. Forms without adhesive structure posterior to female genital pore (except some species of *Cestoplana*). Eyes distributed fanwise over cephalic region, or in tentacular and cerebral clusters, sometimes also in marginal or submarginal bands. Pharynx ruffled. Copulatory complexes posterior to pharynx. Male complex tends to be directed anteriorly from male pore. Vagina often forms loop anteriorly to female pore; uterine canals directed anteriorly on leaving vagina.

Key to acotylean superfamilies

1 Eyes in marginal zones of body; eyes very rarely absent .... ***Stylochoidea***

2 Eyes anteriorly distributed fanwise from cerebral organ only to submarginal zones of body .... ***Cestoplanoidea***

3 Eyes only in region of cerebral organ ..... ***Planoceroidea***

Superfamily **STYLOCHOIDEA** Poche, 1926, emend. Nicoll, 1936

Diagnostic features. With marginal eyes and eyes variably distributed over cephalic region; eyes very occasionally absent.

Key to stylochoid families from African waters

1 Male copulatory complex with prostatoids 2
1′ Without prostatoids 3

2 Prostatoids opening into male antrum; Lang's vesicle U-shaped .... ***Discocelididae***
2′ Prostatoids opening on ventral surface of body; Lang's vesicle sacciform .... ***Polyposthiidae***

3 Prostate interpolated .... ***Cryptocelididae***
3′ Prostate independent 4

4 Eyes include tentacular and cerebral clusters .... ***Stylochidae***
4′ Eyes spreading fanwise from cerebral organ; no tentacular or cerebral clusters .... ***Latocestidae***

Family **POLYPOSTHIIDAE** Bergendal, 1893, emend. Bock, 1913

Diagnostic features Fleshy, oval forms tapering somewhat anteriorly. Eyes occasionally absent. Mouth central; pharynx in mid-third of body; intestinal branches not anastomosing. Male copulatory complex without seminal vesicle or spermiducal bulbs; vasa deferentia well developed, lateral to uterine canals; many pyriform prostatoids variably distributed. Female genital pore anterior or posterior to male pore. Female copulatory complex simple; Lang's vesicle sacciform.

Key to polyposthiid genera from African waters

1 Eyes absent. Ventral epidermal cushion posterior to female pore .... ***Polyphalloplana***
1′ Eyes present. No ventral epidermal pad ... ***Cryptocelides***

Genus *CRYPTOCELIDES* Bergendal, 1890

Diagnostic features. Numerous eyes along anterior margin of body; isolated frontal eyes; two elongate clusters of cerebral eyes, postero-laterally to which lies a pair of tentacular eye-clusters. Male genital pore posterior to female. No prostate; 2 to 8 unarmed prostatoids in rosette around wide male antrum into which they open; vasa deferentia open into anterior prostatoid. Many smaller prostatoids posterior to male pore and opening independently on ventral surface of body. Vagina thrown into anteriorly-directed loop.

Cryptocelides loveni Bergendal, 1890

Locality. On sand and rock at 40 to 133 metres, off Atlantic coast of Morocco, July, 1924 (de Beauchamp, 1951*b*).

Further distribution. Scandinavian waters (Bock, 1913), North Sea and possibly southern Australia (Laidlaw, 1904).

Description. Bock, 1913: 100.

Genus *POLYPHALLOPLANA* Bock, in de Beauchamp, 1951

Diagnostic features. Without eyes. Male copulatory complex with several unarmed pyriform prostatoids in rounded group, and opening ventrally through an ovoid epidermal pad lying posteriorly to female genital pore; no prostate. Female copulatory complex between pharynx and male complex.

Polyphalloplana bocki de Beauchamp, 1951

Locality. 85 metres, off coast of Morocco.

Description. de Beauchamp, 1951*b*: 239.

Family DISCOCELIDIDAE Laidlaw, 1903, emend. Poche, 1926

Diagnostic features. Oval forms without tentacles. Marginal eyes in band of variable extent; two elongate clusters of cerebral eyes lateral to, or merging with, tentacular eye-clusters. Pharynx in mid-third of body; intestinal branches not anastomosing. Common genital atrium may occur; male copulatory complex immediately posterior to pharynx. Vasa deferentia forming a loop posteriorly to female copulatory complex; seminal vesicle feebly developed or not apparent; prostate, when evident, interpolated; penis-papilla variably developed. Many unarmed prostatoids embedded in very thick musculature investing male antrum, into which they open. Vagina long; Lang's vesicle present; uterine canals anteriorly separated.

Key to discocelidid genera from African waters

1 With two external openings to female copulatory complex .... ***Tetratrema***
1′ With single female opening in genital atrium 2
2 One seminal canal opening into genital atrium .... ***Discocelis***
2′ Two seminal canals opening into genital atrium .... ***Paradiscocelis***

Genus *DISCOCELIS* Ehrenberg, 1836, *sensu* Lang (1884)

Diagnostic features. Marginal eyes in anterior third of body. One or two genital pores. Feebly-developed seminal vesicle; ejaculatory duct passes through thick muscular wall of genital atrium, into which it opens; without prostatic vesicle; numerous prostatoids embedded in thick dorsal wall of atrium. Vagina extends dorso-posteriorly from its aperture; Lang's vesicle horseshoe-shaped.

Discocelis tigrina (Blanchard, 1847) Lang, 1884

Polycelis tigrina Blanchard, 1847
Leptoplana tigrina (Blanchard) Diesing, 1850
Elasmodes tigrinus (Blanchard) Stimpson, 1857

Locality. Port Etienne, Mauritania, 9 Nov., 1935 (Palombi, 1939*b*). Also recorded from Mediterranean Sea (Lang, 1884).

Description. Lang, 1884: 467.

Genus *PARADISCOCELIS* gen.nov.

Definition. Discocelididae. Body elongate oval. Marginal eyes confined to anterior third of body; additional eyes in two elongate clusters in cerebral region. Male and female ducts open into genital atrium. Male copulatory complex enclosed in a muscular mass; vasa deferentia unite to form a vesicle lined with a glandular epithelium and giving rise to two sperm-canals opening separately into genital atrium. Pair of large fusiform glandular organs lie in anterior wall of muscular mass and a similar pair in posterior wall, with several small prostatoids lying between the two pairs. Vagina directed posteriorly from genital atrium; Lang's vesicle horseshoe-shaped.

Type-species. *Paradiscocelis furcata* sp.nov.

Paradiscocelis furcata sp.nov.

Type-locality. Inhaca Island, Mozambique (among *Favia* weed and on flats opposite Marine Biol.Stat.—V. Gabie *leg.*). B.M. reg.nos: Holotype 1985.7.3.3; Paratypes 1985.7.3.4–7.

Description (Fig.1). None of the available specimens is fully mature. Body 16–27 mm in length and up to 7 mm in width. According to a water-coloured painting, the dorsal surface in life is pale brown, with underlying intestinal branches showing as dark brown transverse streaks. Very small eyes arranged in two or three irregular rows along anterior margin of body, gradually diminishing to a single row as they extend posteriorly to about level of cerebral organ or a little beyond. Laterally to the cerebral organ, further eyes lie in two elongate clusters with 75 to 90 eyes in each cluster, in which tentacular eyes are the larger and lie nearer to the dorsal surface of the body, somewhat laterally in posterior half of each cluster. Mouth opens into hind region of pharyngeal

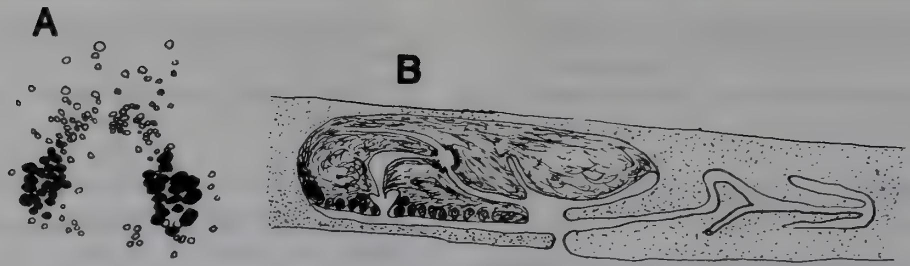

Fig.1 *Paradiscocelis furcata*: A, arrangement of eyes anteriorly; B, sagittal section of copulatory organs.

chamber; pharynx with several pairs of shallow lateral folds lying in mid-third of body.

Common genital pore lies shortly posterior to pharynx and leads into a spacious genital atrium containing openings of male and female ducts. Male complex not yet fully mature, so only a partially-developed structure can be described. The male copulatory complex is invested with a very thick mass of muscle-fibres. An ejaculatory duct appears in the antero-dorsal region of this musculature and is lined with a ciliated epithelium, but it is not possible to determine whether a seminal vesicle will be formed later. In the middle of the muscular mass, the ejaculatory duct widens into a small vesicle lined with glandular cells, suggesting that the vesicle might later function as a prostate. This vesicle gives off two limbs, one directed anteriorly and the other posteriorly. The anterior limb opens into the anterior region of the genital atrium through a wide depression on the ventral surface of the muscular mass, whereas the posterior limb opens through a thick protuberance into the atrium near the genital pore. At each end of the muscular mass lies a pair of relatively large fusiform glandular organs, and between the two pairs a number of pyriform prostatoids lie beneath the surface of the mass and open into the atrium. The latter is wide, but much compressed dorso-ventrally. No penis-papilla has been made out.

From the hind wall of the genital atrium, the vagina extends posteriorly and terminates in a crescentic Lang's vesicle with anteriorly-directed limbs. The vagina has not yet developed a 'shell'-chamber, but about midway along its length, it receives a common uterine canal.

Genus *TETRATREMA* gen.nov.

Definition. Discocelididae, Body elongate oval. Marginal eyes extend posteriorly to various levels, mainly in anterior half of body. Tentacular and cerebral eyes mingle to form two elongate clusters lateral to cerebral organ. Male and female genital pores well separated, additional female pore adjacent and posterior to male pore. Thick muscular dorsal wall of male antrum forms two large symmetrically-disposed bulbs, between which the ejaculatory duct passes to open into the male antrum; many prostatoids lie beneath surface of each bulb. Posterior region of ejaculatory duct is swollen and lined with a glandular epithelium and probably functions as a prostate. Female antrum short, leads into an elongate anterodorsally directed 'shell'-chamber; Lang's vesicle U-shaped.

Type-species. *Tetratrema bifurcatum* sp.nov.

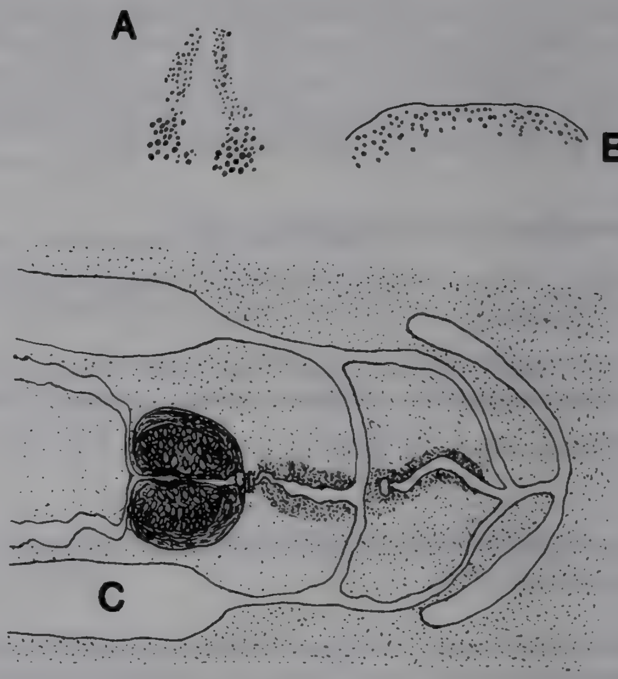

Fig.2 *Tetratrema bifurcatum*: A, tentacular and cerebral eye-clusters; B, anterior marginal eyes; C, ventral view of male and female copulatory complexes.

Tetratrema bifurcatum sp.nov.

Type-locality. Ishmalia, Red Sea (A.El-Ghamery *leg.*) B.M.reg.nos: Holotype 1985.6. 11.1; Paratypes 1985.6.11. 2–5.

Description (Fig.2). Of the specimens available, only one appears to be fully developed and measures 22 mm in length and 14 mm in maximum width. The other specimens are smaller and have reached varying degrees of development; the smallest being 15 mm long and 9 mm wide. Dorsal surface of body brownish, darker towards the pharyngeal region, with a reticulum of darker brown, due to ovaries and oviducts lying beneath the body-wall.

Eyes in two elongate clusters alongside the cerebral organ, which lies at about one-sixth of the body-length from the anterior margin. Each cluster contains cerebral and tentacular eyes; latter darker and larger than former and placed in hind region of each cluster. The two clusters may be distinctly separated or anteriorly confluent. Marginal eyes extend posteriorly to different levels according to size of body; in smallest specimen to level with tentacular eyes, in largest to hind level of pharynx. Pharynx with several pairs of lateral folds and about half as long as body. It extends posteriorly from near cerebral organ to immediately anterior to male copulatory complex. Mouth opens into posterior region of pharyngeal chamber. Intestinal trunk long, extending anteriorly and posteriorly beyond pharynx; it has several pairs of lateral branches.

Testes ventral, ovaries dorsal, to intestinal branches. Vasa deferentia appear to arise laterally to mid-level of pharynx and ventrally to uterine canals. They extend posteriorly to beyond the female copulatory complex, where both limbs turn inwardly to unite in the median line to form a posterior loop. At a level between the pharynx and the male copulatory complex, each vas deferens gives off an inner branch. These branches unite in the median line to form a short ejaculatory duct, the distal region of which is somewhat swollen, lined with a glandular epithelium, and possibly functions as a prostate. Dorsal wall of male antrum strongly muscular and appears as two large symetrically-arranged bulbs. The ejaculatory duct passes between these bulbs to open into the middle of the male antrum. Beneath the ventral surface of each bulb lie numerous small pyriform prostatoids opening into the male antrum.

There are two female genital pores. The main pore lies at about 1 mm posteriorly to the male. It opens into a short antrum leading to an elongate 'shell'-chamber extending posteriorly for a short distance, then bending antero-dorsally to join the vagina interna lined with a tall glandular epithelium. After receiving the common uterine canal, the vagina interna continues posteriorly to open into the base of a U-shaped Lang's vesicle, limbs of which are anteriorly directed.

This new form also possesses an accessory female copulatory complex opening to the exterior immediately posterior to the male pore. The aperture of the accessory complex leads into a shallow antrum from which a relatively wide convoluted canal runs postero-dorsally. The inner two-thirds of this canal is coated with a thick layer of eosinophilic gland-cells resembling 'shell'-glands. The inner end of the canal bifurcates into two laterally-directed branches, each opening into its nearest uterine canal. This accessory complex is confined to the region between the male and female genital pores. The uterine canals extend anteriorly to the ocular region where they remain separated.

NOTE. Again, here is an instance among discocelidid polyclads of where a portion of the ejaculatory duct is swollen and lined with gland-cells, suggesting the existence of a prostate, an organ perhaps appearing late in the development of the male complex.

Family **STYLOCHIDAE** Stimpson, 1857

DIAGNOSTIC FEATURES. Fleshy forms of varying shape and size. Nuchal tentacles in varying degrees of development usually present. Marginal eyes small; many eyes spread over cephalic region, disposed in tentacular and cerebral clusters and sometimes in frontal or cerebro-frontal groups. Pharynx more or less in mid-third of body. Male and female genital pores in posterior third of body. Male copulatory complex usually anterior to male pore; seminal vesicle and/or pair of spermiducal bulbs more or less ventral to independent prostate; penis-papilla elongate or bluntly conical. Vagina often forming an anteriorly-directed loop; its end may function as a genito-intestinal canal, a ductus vaginalis, Lang's vesicle, or fuse with uterine canals.

Key to stylochid genera from African waters

1	Uterine canals open into proximal end of vagina	***Stylochus***	
1′	Vagina extending posteriorly beyond entrance of uterine canals		2
2	Vagina with ductus vaginalis	***Cryptophallus***	
2′	Vagina terminating in Lang's vesicle		3
3	With spermiducal bulbs	***Ancoratheca***	
3′	Without spermiducal bulbs		4
4	Seminal vesicle ventral to prostate	***Leptostylochus***	
4′	Seminal vesicle dorsal to prostate	***Pseudidioplana***	

Genus ***STYLOCHUS*** Ehrenberg, 1836

DIAGNOSTIC FEATURES. Oval or somewhat discoid forms with retractile tentacles. Marginal eyes in band of variable extent; cerebral eyes in a single row or two distinct clusters; tentacular eyes within or below tentacles, frontal eyes often present. Pharynx relatively long, centrally or posteriorly placed. Genital pores approximate, near posterior end of body. Seminal vesicle simple, bipartite or tripartite; prostate large and muscular, lined with tall epithelium thrown into longitudinal, diagonal or radial folds; unarmed penis-papilla stoutly conical, without penis-sheath. Vagina crozier-like or sigmoid in lateral view; 'shell'-chamber with lining often thrown into a spiral fold of four or five turns.

NOTE. In a review of *Stylochus*, du B.-R. Marcus and Marcus (1968) divided the genus into two subgenera: *Stylochus* (*Stylochus*) for species with an entire or undivided seminal vesicle, and *Stylochus* (*Imogine*) for species in which the vesicle and a pair of spermiducal bulbs unite to form a trilobed anchor-shaped structure, regarded as a seminal vesicle. This division of the genus has been generally accepted. As mentioned below, the genus *Distylochus* Faubel, 1983, appears to fall between the subgenera *S.* (*Stylochus*) and *S.* (*Imogine*), thus it is here considered as a subgenus of *Stylochus*.

Key to subgenera of the genus *Stylochus*

1	Seminal vesicle simple	***(Stylochus)***
1′	Seminal vesicle bipartite	***(Distylochus)***
1′	Seminal vesicle tripartite	***(Imogine)***

From available evidence, the structure of the copulatory complexes among species in each subgenus is so uniform that it is rarely possible to separate one species from another on this basis. At present, it seems that the disposition of the cerebral and tentacular eye-clusters, and perhaps the coloration of the tentacles, are means of differentiating species. There seem also to be features in the male complex that require the study of several specimens of a species. Firstly, the size of the seminal vesicle and its comparison with that of the prostate, and the length of the ejaculatory duct in fully mature worms. Secondly, early in its development, the prostate is so packed with a glandular epithelial lining that a lumen is not apparent, but as the organ becomes larger, so a lumen appears and the lining is thrown into folds disposed in a longitudinal, a diagonal or a radial direction. It remains, however, to be seen whether the direction of the folds is constant within a given species. From a comparison of figures of *Stylochus* (*Imogine*) *alexandrinus* given by Steinböck (1937) and by Galleni (1976) it would appear that this is not so.

Because of the uncertainty concerning speciation in the genus *Stylochus*, the following key to species is somewhat artificial, as emphasis has been placed on features which may not be constant among individuals of a species.

Key to species of *Stylochus (Stylochus)* from African waters

1	Vasa deferentia enter seminal vesicle by a common canal	***alexandrinus***
1′	Vasa deferentia open separately into seminal vesicle	2
2	Ejaculatory duct very short	***suesensis***
2′	Ejaculatory duct long	3
3	Dark ring round base of each tentacle	***meixneri***
3′	Tentacles without dark ring	4
4	Frontal eyes present	***sixteni***
4′	Frontal eyes absent	5
5	Prostate oval; epithelial folds radial	6
5′	Prostate pyriform or conical; epithelial folds directed posteriorly	8
6	Marginal eyes round body	***castaneus***
6′	Marginal eyes only in anterior third of body	7
7	Dorsal surface of body salmon-coloured	***salmoneus***
7′	Dorsal surface of body light grey with reddish spots	***djiboutiensis***
8	Cerebral eyes present	***neapolitanus***
8′	Cerebral eyes said to be absent	***zanzibaricus***

Stylochus (Stylochus) suesensis Ehrenberg, 1831

Planocera suesensis Örsted, 1844
Localities. Red Sea (Ehrenberg, 1831); Suez Canal and Gulf of Suez (Palombi, 1928).
Descriptions: Ehrenberg, 1831:36; Palombi, 1928: 582.

Stylochus (Stylochus) alexandrinus Steinböck, 1937

LOCALITIES. eastern harbour, Alexandria, Egypt (Steinböck); Tuscany coast of Italy (Galleni, 1976); Ocean, Morocco (G. Bitar *leg.*).

DESCRIPTIONS. Steinböck, 1937:1; Galleni, 1976:15.

Stylochus (Stylochus) castaneus Palombi, 1939

Stylochus neapolitanus of Laidlaw, 1906.

LOCALITIES. Cape Verde Is (Laidlaw, 1906); 14°40′N., 16°15′W., near Rufisque, Senegal (Palombi).

DESCRIPTIONS. Laidlaw, 1906:707; Palombi, 1939*b*:95.

Stylochus (Stylochus) djiboutiensis Meixner, 1907

LOCALITY. Gulf of Tadjourrah, Djibouti (Meixner).

DESCRIPTION. Meixner,1907: 419.

Stylochus (Stylochus) meixneri Böck, 1925

Stylochus reticulatus (Stimpson, 1855) Meixner, 1907
Stylochus cosieriensis Böck, 1925 (=*reticulatus* Meixner of Meyer, 1922)

LOCALITIES. Grand Reef, Musha I., Gulf of Tadjourrah, Djibouti (Meixner); Kossier, Red Sea (Meyer).

DESCRIPTIONS. Meixner, 1907: 435; Meyer, 1922: 145.

NOTE. As *S. meixneri* and *S. cosieriensis* appear to be morphologically identical, and each bears a dark ring round the base of each tentacle, the species are here considered to be synonymous.

Stylochus (Stylochus) neapolitanus (delle Chiaje, 1841) Lang, 1884

Planaria neapolitana delle Chiaje, 1841

LOCALITIES. Cape Verde Is (Laidlaw, 1906:707).

DESCRIPTIONS. Lang, 1884: 447; Meixner, 1907: 422.

NOTE. Laidlaw (1906) provisionally assigned a specimen from the Cape Verde Is to this species, but Palombi (1939) considered this specimen to belong to *Stylochus castaneus*.

Stylochus (Stylochus) salmoneus Meixner, 1907

LOCALITY. Penguin Reef, Gulf of Tadjourrah, Djibouti (Meixner).

DESCRIPTION. Meixner, 1907: 420.

Stylochus (Stylochus) sixteni Marcus, 1947

Stylochus crassus Böck, 1931, *nec* Verrill, 1892

LOCALITY. Scraped from ship at 30°S., 15°W. It was thought not improbable that the worm became attached to the ship during its stay in the Cape Verde Is (Böck).

DESCRIPTION. Böck, 1931: 263.

Stylochus (Stylochus) zanzibaricus Laidlaw, 1903

LOCALITIES. Zanzibar (Laidlaw); suspected predator of barnacles in New Zealand (Skerman, 1968).

DESCRIPTIONS. Laidlaw, 1930*a*: 105; Meixner, 1907: 425.

NOTE. Both Laidlaw and Meixner express doubt as to this species being distinct from *Stylochus* (*S.*) *neapolitanus*. Laidlaw also states that he did not find 'any definite groups of brain-eyes'.

Key to *Stylochus* (*Imogine*) species from African waters

1	Seminal vesicle feebly developed; without penis-papilla (?)	***minimus***
1′	Seminal vesicle strongly developed; penis-papilla distinct	2
2	Cerebral eyes almost entirely posterior to level of tentacles	***meridianus***
2′	Cerebral eyes equally distant anteriorly and posteriorly to level of tentacles	3
3	Dorsal surface of body greenish yellow; uterine canals branched	***orientalis***
3′	Dorsal surface whitish, speckled with dark brown; uterine canals not branched	***mediterraneus***

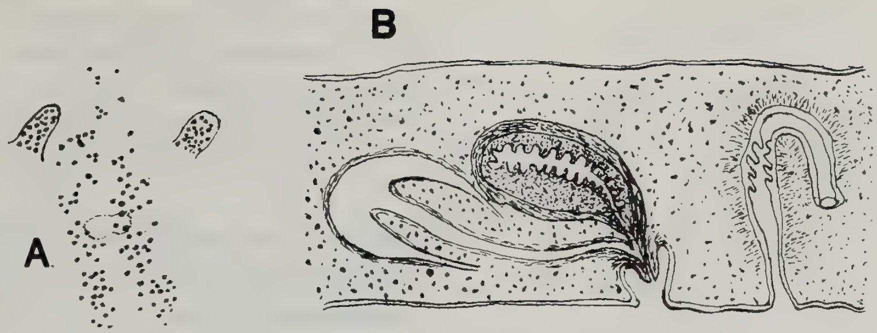

Fig.3 *Stylochus* (*Imogine*) *meridianus*: A, arrangement of tentacular and cerebral eye-clusters; B, sagittal section of copulatory complexes.

Stylochus (Imogine) minimus Palombi, 1940

LOCALITY. Loango, French Equatorial Africa (Congo), June, 1938 (Palombi).

DESCRIPTION. Palombi, 1940: 111 (only specimen available appears to be not fully developed).

Stylochus (Imogine) mediterraneus Galleni, 1976

LOCALITIES. Temara and Ocean, Morocco (G.Bitar *leg.*) Also known from the Tuscany coast of Italy (Galleni).

DESCRIPTION. Galleni, 1976: 15.

Stylochus (Imogine) orientalis Böck, 1913

LOCALITIES. Vicinity of Marine Biol.Stat., Inhaca I., Mozambique (V. Gabie *leg.*) and Eylath, Gulf of Aqaba, Red Sea (H. Steinitz *leg.*). Widely distributed in Indo–West Pacific region, having been recorded from the Gulf of Siam, Formosa Canal and Western Australia (Böck).

DESCRIPTION. Böck, 1913: 128.

Stylochus (Imogine) meridianus sp.nov.

Stylochus sp. Day, Field & Penrith, 1970

LOCALITIES. South Africa. Type-specimen from 12–14 metres, Roman Rock, False Bay, 23.9.1954 (reg.no. 1987.3.31.1); paratypes from Langebaar, Saldanha Bay (reg.no. 1987.3.31. 2–8). *False Bay*: among rocks in 14–17 m, S. of Kogel Bay, 19.8.52; on vertical rock in 4–6 m below LWST; intertidal, in sandy mud, Knysna Estuary, 18.7.47. *Saldanha Bay*: intertidal, Lynch Point, 22.9.57; on fine khaki sand in 22 m, 33°02′S., 17°57.4′E., 25.4.62; in mud on *Zostera* bed at Oesterval, Langebaan, 3.5.61; on mud, Langebaar, 28.4.49. *Durban Bay*: scraped from buoy at junction of Maydon and Congella Channels, 24.4.54.

DESCRIPTION. (Fig.3). Body broadly oval in outline, measuring up to 12 mm in length and 10 mm in width, or more or less discoid 8–10 mm in diameter. Dorsally, the living worm is brownish or brownish with dark speckles, but one specimen had ‘abundant dorsal coloration (black)’. 20 to 60 eyes lie within and at the base of each well-developed tentacle; cerebral eyes arranged in two elongate clusters often posteriorly confluent, mainly posterior to level of tentacles; marginal eyes around body, disposed in a band of four or five irregular rows anteriorly, decreasing to a single, double or triple row along the posterior margin. Cerebral organ distinctly posterior to level of tentacles.

As in most other species of *Stylochus*, the ventral subepidermal musculature in about three times deeper than that of the dorsal, owing to a very thick layer of longitudinal muscles.

Mouth centrally placed; pharynx with about 7 pairs of lateral folds in mid-third of body. In preserved specimens, the male copulatory complex may be well separated from the pharynx. Testes ventral, ovaries dorsal, but in the region of the copulatory organs they tend to mingle with each other.

Trilobed or anchor-shaped seminal vesicle well developed, lying anteriorly to the prostate; median lobe of vesicle is narrowest and soon becomes the ejaculatory duct. Prostate oval, with a thick muscular wall through which pass efferent ducts of extracapsular gland-cells opening into its lumen; its epithelial lining is thrown into several radial folds, leaving a narrow lumen. Penis-papilla broadly conical. The vagina has a crozier-like outline in lateral view, with a short female antrum and a well-developed ‘shell’-chamber for much of its length. Part of the lining of the ‘shell’-chamber, when fully developed, is thrown into a spiral fold of three or four turns. When the female complex is fully developed, a system of branching uterine canals may be apparent in whole specimens cleared in methyl salicylate and depicted by Böck (1913) in *Stylochus orientalis*. However, before the branching system appears, the usual two canals extend anteriorly where they remain separated.

Genus *STYLOCHUS* Subgenus (*DISTYLOCHUS* Faubel, 1983)

As mentioned above, du Bois-Reymond Marcus and Marcus (1968) divided the genus *Stylochus* (*sensu lato*) into two subgenera: *S.* (*Stylochus*) for those species with an undivided seminal vesicle; and *S.* (*Imogine*) for those species with a muscular trilobed vesicle. This subgeneric division was accepted by Faubel (1983), but for species with a bilobed seminal vesicle constricted into a muscular distal chamber and a non-muscular proximal chamber he erected a new genus *Distylochus*, with *Stylochus pusillus* as its type-species. Since *Distylochus* clearly falls between the two above-mentioned subgenera, the genus is here relegated to subgeneric rank with *Stylochus* (*Distylochus*) containing *S.* (*D.*) *pusillus* Böck, 1913, *S.* (*D.*) *martae* Marcus, 1947, and *S.* (*D.*) *isifer* du Bois-Reymond Marcus, 1955.

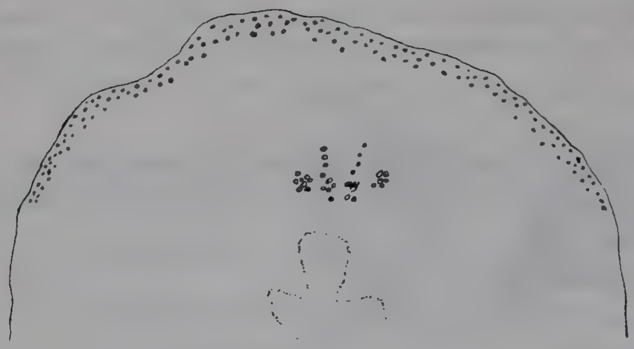

Fig.4 *Stylochus* (*Distylochus*) *martae*, anterior region of body.

Stylochus (Distylochus) martae Marcus, 1947

Note (Fig.4). Two specimens available agree very well with the single specimen described by Marcus (1947), except in the number of cerebral eyes which vary from 4 to 9 in each row.

Locality. Kisny dockyard, Freetown, Sierra Leone, July 1976. Also known from Praia da Enseada, Ilha de Sto.Amaro, 15 km southeast of Santos, Brazil.

Stylochus (s.1.) sp.innom.

Stylochus suesensis Ehrenberg of Laidlaw, 1903*a*

Locality. Ras Oswemba, Zanzibar (Laidlaw, 1903*a*).

Note. Laidlaw's description is inadequate and Palombi (1928) implied that Laidlaw's specimen is not comparable with *Stylochus suesensis* because its marginal eyes are in a continuous series round the body, whereas in Ehrenberg's species they are not. At present it seems reasonable to accept Palombi's opinion as some of his specimens were collected in the Gulf of Suez and Ehrenberg's specimen came from the Red Sea.

Stylochus (s.1.) sp.innom.

Stylochus neapolitanus (Delle Chiaje) Laidlaw, 1906

Locality. on lighters, in crevices of compound ascidians or in empty lamellibranch shells, Cape Verde Is, North Atlantic (Laidlaw, 1906).

Note. No details of the copulatory organs were given by Laidlaw, who said 'I have some doubts as to whether this species is really identical with the Mediterranean *S. neapolitanus*.' Palombi (1939*b*), however, considered Laidlaw's specimens to be *Stylochus castaneus*. There is nevertheless, one feature in the Cape Verde specimens which may distinguish them from both *S. neapolitanus* and *S. castaneus*, namely, the tentacles, which are dark grey in contrast to the colour of the dorsal surface of the body. In *S. neapolitanus* each tentacle is ringed with a band of vermillion, and the tentacles of *S. castaneus* are of a chestnut colour. Therefore, it seems advisable to regard Laidlaw's form as an indeterminate species of *Stylochus*, until more specimens from Cape Verde Is become available for study.

Genus *ANCORATHECA* Prudhoe, 1982

Diagnostic features. Body oval. Marginal eyes in band of variable extent; cerebro-frontal eyes widely distributed; tentacular eyes in two small clusters among c.f. eyes. Pharynx in mid-third of body. Genital pores near posterior end of body. Seminal vesicle trilobed or anchor-shaped; prostate well developed, elongate, with smooth shallow epithelial lining; penis-papilla with stylet in penis-pocket with shallow penis-sheath. Vagina forming a loop, ending in Lang's vesicle which may open on ventral surface of body.

Ancoratheca pacifica (Böck, 1923) Prudhoe, 1982

Neostylochus pacificus Böck, 1923
Neostylochus sp.nov. Day, Field & Penrith, 1970
Localities: Cape Province, South Africa (Saldanha Bay, Port Elizabeth, common in False Bay). Also known from Juan Fernandez Is, off coast of Chile, South America (Böck, 1923)

Description. Böck, 1923:342.

Note. (Fig.5). The South African specimens agree very well with Böck's description. The many specimens available are in various stages of development and one noticeable feature is the presence of two groups of tentacular eyes enclosed by numerous cerebro-frontal eyes in mature specimens, and the absence of such eyes in immature worms, as shown in fig. In young specimens, the cerebro-frontal eyes tend to run in streaks, presumably along nerves radiating from the cerebral organ. Usually, the genital pores are placed very close to one another, but in some specimens the tissue around them is so contracted as to form a deep depression on the ventral surface of the body to give the appearance of the male and female ducts opening into an antrum.

Genus *CRYPTOPHALLUS* Böck, 1913

Diagnostic features. Broadly-oval fleshy forms with shallow tentacles containing eyes. Marginal eyes extend round body; cerebral eyes in one or two elongate groups merging with frontal eyes. Pharynx long. Genital pores widely separated. Male copulatory complex relatively small; spermiducal bulbs pyriform or elongate; no seminal vesicle; small pyriform prostate disposed vertically to male pore and posteriorly to spermiducal bulbs, epithelial lining shallow and slightly ridged; ejaculatory duct short; conical penis-papilla short, thick, without penis-sheath. Vagina thrown into anteriorly-directed loop; ductus vaginalis opening into female antrum.

Cryptophallus wahlbergi Böck, 1913

Cryptophallus aegyptiacus Melouk, 1940

Localities. Umtwalumi, Natal, South Africa, 27.12.1938 (Day colln.). Port Natal, Durban, S. Africa (Böck); El Ataka, Gulf of Suez and Ghardaga, Red Sea (Melouk).

Description. Böck, 1913: 120; Melouk, 1940:125.

Note. The male complex, as figured by Melouk, appears to be partially everted, thus showing the prostatic duct and the ejaculatory duct to open to the exterior independently of each other. When compared with other species of *Cryptophallus*, there seems to be very little doubt that the condition figured has been brought about by contraction of the body at fixation, and that *C. aegyptiacus* is otherwise comparable with *C. wahlbergi*.

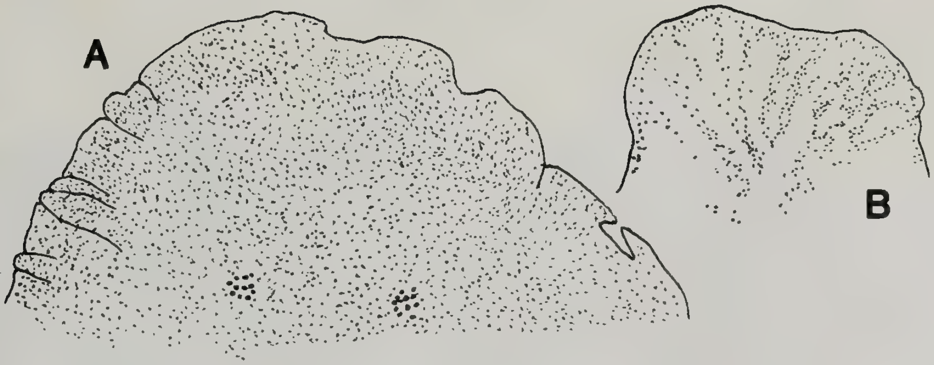

Fig.5 *Ancoratheca pacifica*, anterior region of body: A, mature specimen; B, immature specimen.

Genus *LEPTOSTYLOCHUS* Böck, 1925

DIAGNOSTIC FEATURES. Body oval or elongate. Tentacles weakly developed or apparently absent. Tentacular eyes may merge with cerebral eyes; marginal eyes in anterior half of body. Pharynx in mid-third of body and has several pairs of lateral folds. Genital pores close to each other, situated posteriorly. Spermiducal bulbs present; no seminal vesicle; elongate or pyriform prostate horizontally disposed dorsally to ejaculatory duct; epithelial lining of prostate in radial folds; penis-papilla small, unarmed. Vagina long, thrown into an anteriorly-directed loop; Lang's vesicle bulbous.

Leptostylochus capensis Palombi, 1938

Leptostylochus sp.? Palombi, 1936.

LOCALITIES. Cape Province, South Africa. Still Bay and False Bay (Day colln.); Praekstoel (Palombi, 1936); St. James and Reef Bay, Port Elizabeth (Palombi, 1938); Bat's Cave Rock, East London (Palombi, 1939).

REFERENCES. Palombi, 1938: 334, 1939*a*: 125.

Genus *PSEUDIDIOPLANA* gen.nov.

DIAGNOSTIC FEATURES. Stylochidae with oval body and conical tentacles containing numerous eyes crowded near apex; several small cerebral eyes scattered between tentacles; marginal eyes in anterior half of body. Pharynx centrally situated. Genital pores close to each other in hind third of body. Thin-walled vasa deferentia open separately into spacious seminal vesicle. Large globular prostate ventral to seminal vesicle and lined with an epithelium thrown into several deep folds mainly diagonally disposed. Ejaculatory duct and prostatic duct at base of unarmed penis-papilla. Lang's vesicle probably horseshoe- or anchor-shaped.

TYPE-SPECIES. *Pseudidioplana palombii* (Faubel, 1983).

Pseudidioplana palombii (Faubel, 1983) nov.comb.

Idioplana australiensis Woodworth of Palombi (1928)
Leptostylochus palombii Faubel, 1983

LOCALITY. Suez (Port Taufig), Egypt (Palombi).

DESCRIPTION. Palombi, 1928:586.

NOTE. Palombi's specimen appears not to be identical with *Idioplana australiensis* Woodworth, 1898, originally described from the Australian Great Barrier Reef. In fact, as the present writer (1952) points out, it bears a closer morphological resemblance to species of the genus *Idioplanoides* Barbour, 1912, than to those of the genus *Idioplana* Woodworth. Faubel (1983) also considers Palombi's identification to be erroneous and placed *Idioplana australiensis* of Palombi in the genus *Leptostylochus* under a new name *Leptostylochus palombii*. However, Palombi's specimen is certainly not congeneric with the type-species of *Leptostylochus*, *L. elongatus* Bock, 1925, which has a pair of spermiducal bulbs and a prostate lying dorsally to a seminal vesicle, features not found in Palombi's specimen. It is perhaps opportune to mention that according to Faubel's definition of *Idioplana*, the genus possesses a seminal vesicle and an anchor-shaped Lang's vesicle. But Woodworth (1898) indicated that in the type-specimen of *Idioplana australiensis* the male copulatory complex includes a pair of spermiducal bulbs ('vesiculae seminales'), no seminal vesicle, and Lang's vesicle is bulbous, not horseshoe- or anchor-shaped. It would seem that Faubel has based his conception of *Idioplana* on *Idioplanoides insignis* (Laidlaw, 1904) and *Idioplanoides atlantica* (Böck, 1913), but *Idioplanoides* is clearly distinct from *Idioplana*.

Family **LATOCESTIDAE** Laidlaw, 1903

DIAGNOSTIC FEATURES. Elongate to ribbon-like forms without tentacles. Numerous eyes scattered fanwise, often in streaks, over cephalic region of body; marginal eyes usually present. Mouth and ruffled pharynx centrally or posteriorly situated. Genital pores separated, near hind end of pharynx. Male copulatory complex directed more or less anteriorly from male pore. Relatively large prostate independent, usually dorsal to ejaculatory duct and provided with a tall epithelial lining; prostatic duct and ejaculatory duct unite before entering thick, conical, penis-papilla lying in a penis-pocket or shallow male antrum. Vagina narrow, thrown into an anteriorly-directed loop; Lang's vesicle or ductus vaginalis present.

Genus *LATOCESTUS* Plehn, 1896

DIAGNOSTIC FEATURES. Body narrowing towards extremities. Marginal eyes, assumed absent in type-species, *L. atlanticus*, in band of variable extent; further eyes disposed fanwise from posterior to cerebral organ. Pharynx in mid-third of body;

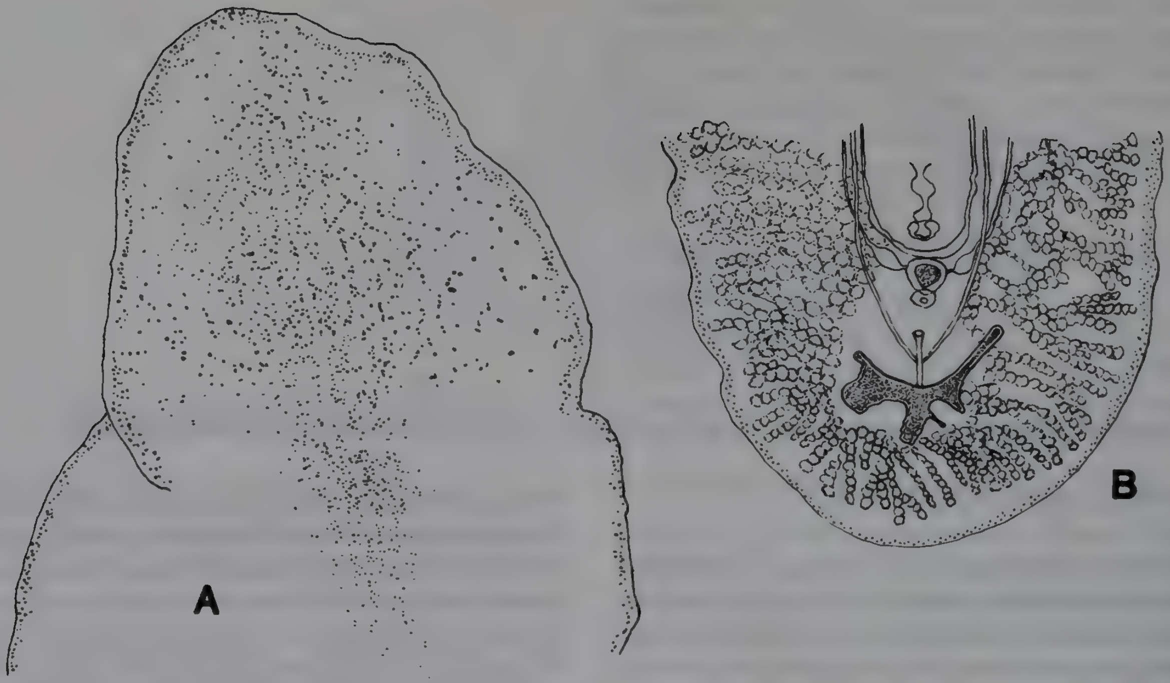

Fig.6 *Latocestus plehni*: A, eyes in anterior region of body; B, reproductive organs and intestinal branches (ventral view).

anterior branch of intestinal trunk long; intestinal branches not anastomosing. Usually with spermiducal bulbs, efferent ducts of which unite to form long ejaculatory duct; prostate pyriform; small unarmed penis-papilla in male antrum. Lang's vesicle bulbous or somewhat U-shaped; uterine canals not anteriorly confluent.

Key to *Latocestus* species from African waters

1 Without marginal eyes .... ***atlanticus***
1′ With marginal eyes 2

2 Lang's vesicle elongate .... ***marginatus***
2′ Lang's vesicle irregularly bulbous or somewhat crescentic .... ***plehni***

Latocestus atlanticus Plehn, 1896

LOCALITIES. Atlantic Ocean (Cape Verde Is, type-locality) and Rio de Janeiro, Brazil (Plehn).

DESCRIPTION. Plehn, 1896*a*: 159.

NOTE. Although material from two localities was originally available, Plehn's (1896) description contains no mention of the presence of marginal eyes, and because of this it appears to have been assumed by subsequent writers that *L. atlanticus* is a species without marginal eyes. It should, however, be stressed that marginal eyes in *Latocestus* are sometimes exceedingly small, and were very likely overlooked by Plehn.

Latocestus marginatus Meixner, 1907

LOCALITY. Among *Zoanthus* colonies in Gulf of Tadjourrah, Djibouti, 7.2.1904.

DESCRIPTION. Meixner, 1907: 461.

Latocestus plehni Laidlaw, 1906

LOCALITIES. East Beach, Pram Pram, Ghana, 30.1.1949 (B.M.(N.H.) colln.); in deep crevices of nullipore or in shells, Cape Verde Is (Laidlaw); among algae, Malembo, Angola (Palombi).

DESCRIPTION. Laidlaw, 1906: 711; Palombi, 1940: 110.

DESCRIPTIVE NOTE (Fig.6). Laidlaw's account of this species is most inadequate, and Palombi examined only a juvenile specimen. The specimens from Ghana measure up to 30 mm in length and 6 mm in width. In life, they were 'dirty brownish pink', but after preservation in alcohol, they are now light brown tinged with pink. Distribution of eyes in anterior region of body as shown in Fig.6; marginal eyes in band around body. Mouth opens into hind region of pharyngeal chamber. Two narrow thin-walled vasa deferentia, each of which is posteriorly modified into a muscular spermiducal bulb before uniting to form a long ejaculatory duct. Muscular pyriform prostate dorsal to ejaculatory duct and lined with a tall glandular epithelium thrown into thick radial folds. Ejaculatory duct and prostatic duct unite before entering the male antrum through a broad, but shallow, unarmed penis-papilla. Male pore at about 1.5 mm from posterior end of body in largest specimen.

Female aperture at about 0.5 mm posterior to male pore. Vagina externa thrown into a short anteriorly-directed loop before bending posteriorly to receive common uterine canal and continuing as the vagina interna to shortly terminate in U-shaped Lang's vesicle with an irregular posterior outline, as shown in Fig.6. Epithelium of vagina interna or 'stalk' of Lang's vesicle has a number of radial folds to give its lumen a moniliform appearance. Epithelium of 'shell'-chamber thrown into a spiral fold of four or five turns.

Morphologically, the Ghanaian specimens very closely resemble *Latocestus atlanticus*. In fact, were it not for the supposed absence of marginal eyes in Plehn's species, it would be justifiable to accept that *atlanticus* and *plehni* are identical.

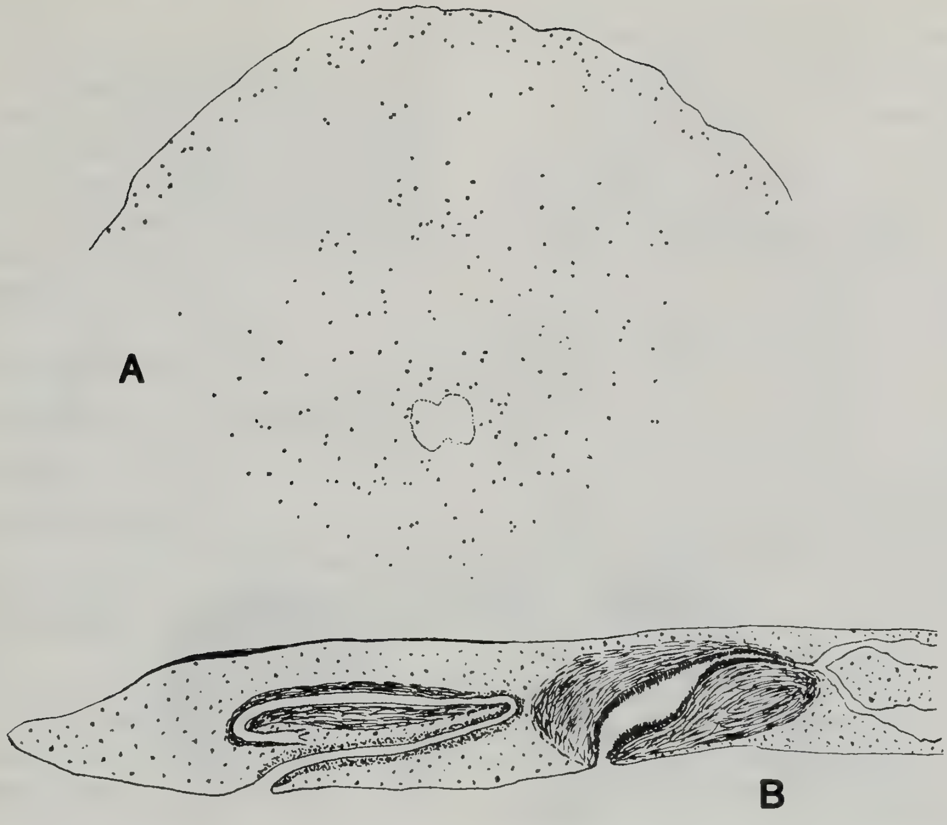

Fig.7 *Cryptocelis capensis*: A, eyes in anterior region of body; B, sagittal section of copulatory organs.

Family CRYPTOCELIDIDAE Laidlaw, 1903, emend. Poche, 1926

DIAGNOSTIC FEATURES. Elongate oval or discoid forms. Tentacles indistinct or not apparent. Marginal eyes small; additional eyes distributed fanwise anteriorly or disposed in cerebral tentacular and frontal groups. Mouth in mid-third of body; pharynx ruffled; intestinal trunk relatively short. Genital pores in mid or hind third of body. Male copulatory complex closely posterior to pharynx and anterior to male genital pore; prostate variously developed, interpolated. Vagina short, sometimes with Lang's vesicle.

Key to cryptocelidid genera in African waters

1	Dorsal surface of body papillate	***Ommatoplana***
1′	Dorsal surface smooth	2
2	With ductus vaginalis	***Neocryptocelis***
2′	Without ductus vaginalis	***Cryptocelis***

Genus *CRYPTOCELIS* Lang, 1884

DIAGNOSTIC FEATURES. Oval fleshy forms without tentacles. Marginal eyes in band of variable extent; frontal eyes may be absent; cerebral and frontal eyes may merge into a widespread mass; tentacular eyes may be well differentiated, or not readily distinguishable from cerebral eye-clusters. Pharynx in mid-third of body; intestinal branches not anastomosing. Vasa deferentia or spermiducal bulbs open into large prostate divided into a glandular proximal or anterior chamber, epithelial lining of which is thrown into deep radial folds, and a sinuous distal or posterior chamber lined with a smooth or slightly folded epithelium; penis-papilla weakly developed or not apparent. Vagina simple, directed anteriorly from female pore; without Lang's vesicle; 'shell'-chamber spacious.

Cryptocelis capensis sp.nov.

LOCALITY. Cape Province, South Africa (on sandy bottom in 24 metres, False Bay 34°10′S, 18°27.5′E.) (Day colln.) Holotype B.M. reg.no. 1987.3.11.7; paratypes 1987.3.11.8–9.

DESCRIPTION (Fig.7). Body of holotype is oval, broadly rounded anteriorly and narrowing posteriorly. It measures 17 mm long and 8 mm wide. Marginal eyes extend round body; additional very small eyes lie posteriorly to cerebral organ and spread fanwise anteriorly to sometimes reach marginal eyes. Mouth at about 11 mm from anterior margin of body and opening into third quarter of pharyngeal pocket; pharynx about 9 mm long, centrally placed, with several pairs of lateral folds; intestinal branches not anastomosing.

Male and female genital pores close together in posterior region of body. Testes ventral to intestinal branches, ovaries dorsal. Swollen vasa deferentia extend posteriorly alongside the pharynx and narrowing considerably in their distal regions to unite and form a short ejaculatory duct leading into a very muscular oval mass. At its junction with the muscular mass, the ejaculatory duct is invested with eosinophilic gland-cells. The duct, still invested with gland-cells, passes into the muscular mass for a short distance, widens, and is then lined with an epithelium of large gland-cells bearing long cilia. This epithelium shows signs of perhaps being thrown into folds later in its development. The duct, now the lumen of the muscular structure, continues its course ventrally. The cilia of the duct become longer and appear to be coated with an eosinophilic material to give this region of the male complex the false impression of being lined with slender bristles. On approaching the ventral surface of the body, the lumen

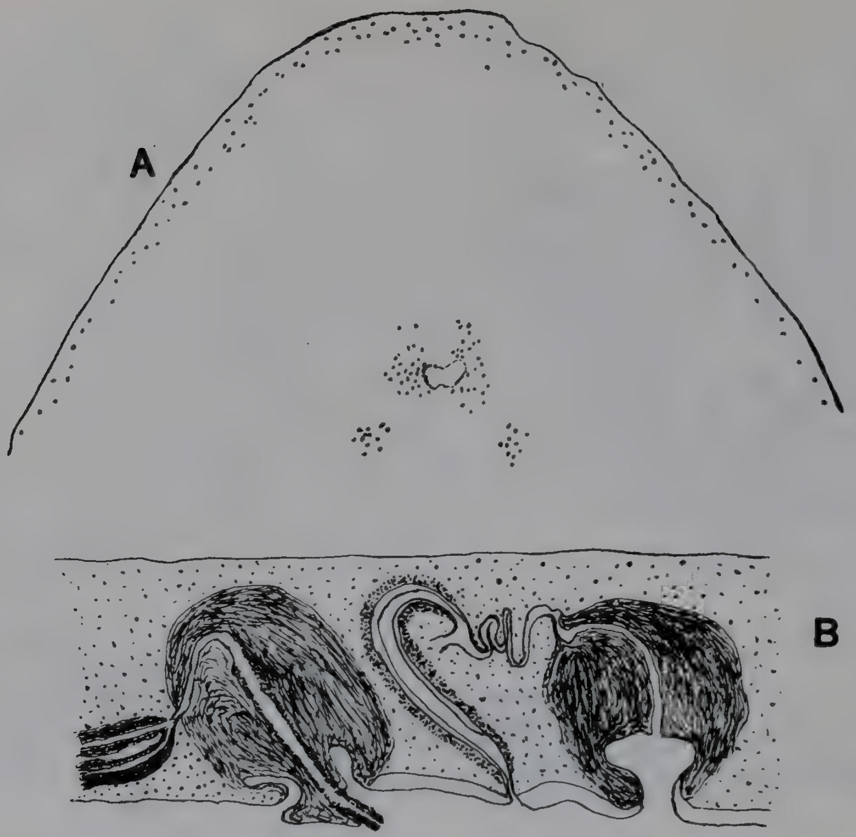

Fig.8 *Neocryptocelis dayi*: A, eyes in anterior region of body; B, sagittal section of copulatory organs.

narrows and opens directly to the exterior. Male antrum absent. The oval muscular mass appears to represent the prostate.

Female antrum narrow and shallow. Vagina thrown into an anteriorly-directed loop, its antero-dorsal portion functioning as a 'shell'-chamber, whereas the posteriorly-directed portion is exceedingly muscular and represents the vagina interna. Uterine canals open directly into the proximal end of the vagina.

NOTE. The fact that the vasa deferentia unite before passing into the male copulatory complex by a common canal agrees with *Cryptocelis alba* Lang and *C. compacta* Lang, but differs from them in the distribution of eyes in the cephalic region.

Genus ***NEOCRYPTOCELIS*** gen.nov.

DIAGNOSTIC FEATURES. Cryptocelididae. Elongate-oval forms without tentacles. Cerebral and tentacular eyes in separate clusters; marginal eyes confined to anterior region of body. Genital pores separated in hind region of body; elongate spermiducal bulbs open independently into pyriform prostate, the lumen of which is divided into two sections. Vagina thrown into an anteriorly-directed loop, with ductus vaginalis.

TYPE-SPECIES. *Neocryptocelis dayi* sp.nov.

Neocryptocelis dayi **sp.nov.**

LOCALITY. On fine sand in 22 metres, 33°02′S, 17°57.4′E, Saldanha Bay, South Africa, 25.4.1962. (Day colln.). Holotype B.M. reg.no. 1987.3.11.1.

DESCRIPTION (Fig.8). Elongate-oval body 17 mm long and 6 mm wide, broader anteriorly than posteriorly; without tentacles. Few very small eyes arranged in paired cerebral and tentacular clusters; marginal eyes in band extending posteriorly to level with tentacular clusters. Pharynx narrow, mainly in posterior half of body and with shallow lateral folds.

Male and female genital pores about 0.5 mm apart in hind region of body. Distal region of each vas deferens is modified as an elongate spermiducal bulb. From each bulb, a narrow duct passes into a pyriform muscular organ and travels dorsally to open into a narrow lumen of the organ. This structure is really a prostate, for its lumen is lined with a low eosinophilic epithelium. In the only specimen available, the distal portion of the prostate is protruded through the male genital pore as a papilla, probably due to contraction of the body at fixation. The epithelial lining of the distal region contains many large gland-cells that stain deeply with haematoxylin. This region, as already mentioned, has everted itself so that its surface appears covered with rings of deeply-stained cells.

Vagina thrown into an anteriorly-directed loop, much of which functions as a 'shell'-chamber. On turning posteriorly, the vagina receives the common uterine duct and continues as a narrow convoluted ductus vaginalis passing through a globular mass of muscles to enter a spacious chamber opening on the ventral surface of the body.

NOTE. The shape of the body, the arrangement of the eyes and the interpolated prostate indicates that the above-described specimen belongs to the family Cryptocelididae and is closely related to the genus *Cryptocelis* Lang. Although its male copulatory complex appears not to be fully developed and is probably somewhat distorted, the structure of the female complex sets it apart from all previously-known cryptocelidids. Therefore, a new genus has been erected for its reception.

Genus *OMMATOPLANA* Laidlaw, 1903

DIAGNOSTIC FEATURES. Fleshy, broadly-oval forms with dorsal tubercles. Marginal eyes in anterior third of body; numerous small eyes scattered in irregular groups over cephalic region. Mouth central. Genital ducts open into atrium near mouth. Seminal vesicle? Prostate assumed to be interpolated, with thick muscular wall and tall epithelial lining containing longitudinal canals. Penis-papilla unarmed, enclosed in penis-pocket. Lang's vesicle present.

Ommatoplana tuberculata Laidlaw, 1903

LOCALITY. Prison Island, Zanzibar, 4.6.1901 (Laidlaw).

DESCRIPTION. Laidlaw, 1903*a*: 111.

NOTE. Type-specimen probably immature.

Superfamily **PLANOCEROIDEA** Poche, 1926, emend. Nicoll, 1935

DIAGNOSTIC FEATURES. Acotylea without marginal eyes; with paired cerebral and tentacular eye-clusters in four separate clusters or in two elongate clusters lateral to the cerebral organ. Pharynx ruffled.

Key to planoceroid families from African waters

1	Male complex with cirrus	2
1′	Male complex without cirrus	3
2	Prostate independent	***Planoceridae***
2′	Prostate interpolated	***Gnesiocerotidae***
3	Prostate independent	***Callioplanidae***
3′	Prostate interpolated	***Leptoplanidae***

Family **LEPTOPLANIDAE** Stimpson, 1857

DIAGNOSTIC FEATURES. Body variable in outline, often somewhat cuneate. Mouth central or in hind half of body. Genital pores generally separated posteriorly to pharynx. Male copulatory complex anterior to male pore; often with muscular seminal vesicle; sometimes with spermiducal bulbs. Prostate variably developed, from bulbous muscular organ to portion of the ejaculatory duct lined or invested with eosinophilic gland-cells. Vagina narrow, usually forming anteriorly-directed loop; Lang's vesicle or ductus vaginalis may be present.

Key to leptoplanid subfamilies from African waters

1	Prostate tubular, sometimes indistinct or moderately differentiated from ejaculatory duct	***Leptoplaninae***
1′	Prostate muscular and vesicular	***Stylochoplaninae***

Subfamily **LEPTOPLANINAE** Marcus, 1947

DIAGNOSTIC FEATURE. Without vesicular prostate.

Key to leptoplanine genera from African waters

1	Tubular prostate with appendix at its inner end	***Leptoplana***
1′	Tubular prostate without appendix	2
2	No seminal vesicle; no Lang's vesicle	***Haploplana***
2′	With seminal vesicle; Lang's vesicle present	3
3	Paired spermiducal bulbs united with elongate seminal vesicle	***Phylloplana***
3′	No spermiducal bulbs	4
4	Female antrum with small bursa	***Pulchriplana***
4′	Female antrum without bursa	***Discoplana***

Genus *LEPTOPLANA* Ehrenberg, 1831, *sensu* Lang (1884)

DIAGNOSTIC FEATURES. Body oval, often broad anteriorly and narrowing posteriorly; without tentacles. Eyes in paired tentacular and cerebral clusters. Pharynx central. Genital pores separated, between them lies an adhesive depression with muscular margin. Vasa deferentia unite to open into muscular seminal vesicle; prostate tubular, with lateral or ventral diverticulum proximally; unarmed penis-papilla inconspicuous lying in long narrow penis-pocket; male antrum shallow. Thick musculature invests male copulatory organs. Lang's vesicle variably developed; uterine canals anteriorly confluent when fully developed.

Leptoplana hyalina Ehrenberg, 1831

LOCALITY. Tor, Red Sea (Ehrenberg).

NOTE. This species, known only from the Red Sea, is the type-species of the genus *Leptoplana*, but is unrecognizable. Lang (1884), however, considered it to be comparable with *Planaria tremellaris* Müller, 1774, from Norway, and it is on this opinion that *Leptoplana* has been generally accepted as a recognizable genus. Bock (1913) doubts this synonymy, and a close examination of the problem shows that *L. tremellaris* is a North Atlantic form with a southern distribution extending into the Mediterranean Sea. It is not known in the Indian Ocean. Since Lang gave no evidence to support his conclusion, it seems that the synonymy of *Planaria tremellaris* and *Leptoplana hyalina* is exceedingly doubtful. Nevertheless, it seems that usage supports Lang's conception of the genus *Leptoplana* with *tremellaris* as its type-species.

Leptoplana tremellaris (Müller, 1774) Örsted, 1843

LOCALITIES. Port Said, Egypt, 13.12.1924 (Palombi, 1928); several localities on Moroccan coast (G. Bitar *leg.*). Common along European coast from Norway to the Mediterranean.

DESCRIPTION. Bock, 1913:181; Faubel, 1983:84.

Genus *DISCOPLANA* Bock, 1913

DIAGNOSTIC FEATURES. Large oval forms without tentacles. Eyes in separated pairs of cerebral and tentacular clusters. Pharynx centrally situated. Genital pores well separated. Seminal vesicle pyriform or elongate; ejaculatory duct extends from seminal vesicle to penis-papilla without forming distinct prostate, but at height of male phase parts of the male complex are thickly coated with extracapsular eosinophilic gland-cells. Penis-papilla distinct and muscular. Vagina narrow; Lang's vesicle bulbous or crescentic.

NOTE. It seems necessary to re-establish the validity of the genus *Discoplana*, because Hyman (1953) considered it to be a synonym of the genus *Euplana* Girard, 1893. Furthermore, Faubel (1983) also rejected *Discoplana* and distributed its species among two families and three genera, two of which were said to be 'new.' Between them, Bock (1913) and Kato (1935 & 1943) assigned six species to the genus, namely, *gigas* (Schmarda, 1859) (type-species), *pacificola* (Plehn, 1896), *malayana* (Laidlaw, 1903), *concolor* (Meixner, 1907), *takewakii* Kato, 1935 and *longipenis* Kato, 1943. The type-species is readily distinguished from that of *Euplana*, *E. gracilis* (Girard), by the presence of a distinct penis-papilla and Lang's vesicle, features here regarded as generically important. The dissolution of *Discoplana* by Faubel is untenable because he has named the type-species of that genus as the type-species of a new genus, *Ilyella*, which is therefore invalid and a synonym of *Discoplana*. Of the remaining species of this genus, Faubel erected the genus *Euilyoida* for *D. takewakii*, presumably because two small spines are said to lie in the efferent duct of the penis-papilla; *D. longipenis* was transferred by Faubel to the genus *Aprostatum* Bock, 1913, which, according to the re-description of its type-species, *A. stiliferum*, given by Marcus (1954), is most certainly not congeneric with *longipenis*. The remaining species of *Discoplana*, namely, *pacificola*, *concolor* and *malayana*, were placed by Faubel in a new genus, *Euplanoides*, with *pacificola* as its type-species. It seems that he differentiated these from *gigas* because in the latter the epithelium of the male antrum contains eosinophilic gland-cells, presumably of a prostatic nature, whereas such gland-cells have not been described in the other species. Because a prostatic lining to a portion of the ejaculatory duct (*sensu lato*) and extracapsular gland-cells often appear late in the development of the male phase among leptoplanid polyclads that have no vesicular prostate, it would seem that the genus *Euplanoides* might be of doubtful validity.

Key to *Discoplana* species from African waters

1 With penis-pocket; Lang's vesicle bulbous ..... ***concolor***
1′ Penis-pocket absent; Lang's vesicle U-shaped or crescentic .... ***gigas***

Discoplana concolor (Meixner, 1907) Bock, 1913

Leptoplana concolor Meixner, 1907
Euplana concolor (Meixner) Hyman, 1954b.

LOCALITY. On a madrepore reef, Musha I., Gulf of Tadjourrah, Djibouti (Meixner).

DESCRIPTION. Meixner, 1907: 452.

Discoplana gigas (Schmarda, 1859) Stummer-Traunfels, 1933

Leptoplana gigas Schmarda, 1859
Leptoplana subviridis Plehn, 1896*a*
Leptoplana pardalis Laidlaw, 1902
Discoplana subviridis (Plehn) Bock, 1913
Susakia badiomaculata Kato, 1934

LOCALITY. Under stones, Recif de la Clochetterie, near Obok, Djibouti (Meixner). Also known from Sri Lanka, Indonesia, Maldive Is, Indian Ocean and Funafuti I., Pacific Ocean, Somalia, Bonin and Gilbert Is, and Japan.

DESCRIPTIONS. Schmarda, 1859:xii,17; Plehn, 1896*a*:330; Laidlaw, 1902:278; Meixner, 1907:457; Bock, 1913:220; Stummer-Traunfels, 1933:3492; Kato, 1934:125.

Genus ***PHYLLOPLANA*** Laidlaw, 1903

Indiplana Stummer-Traunfels, 1933

DIAGNOSTIC FEATURES. Oval forms without tentacles. Eyes in paired cerebral and tentacular groups or in two elongate clusters. Pharynx mainly in anterior half of body; intestinal branches not anastomosing. Separate genital pores in mid-third of body. Elongate spermiducal bulbs fusing with highly muscular portion of ejaculatory duct to form a trilobed or anchor-shaped seminal vesicle. Prostatic glands invest portion of narrow ejaculatory duct to function as a cylindrical prostate. Penis-papilla distinct and may bear stylet. Vagina thrown into an anteriorly-directed loop; Lang's vesicle small.

NOTE. Faubel (1983) maintains *Indiplana* as a valid genus and places it in the family Leptoplanidae because it has the 'male' complex enclosed in massive muscular bulb, whereas he places *Phylloplana* in the family Stylochoplanidae which lacks such a bulb. A careful examination of Stummer-Traunfels description and figure of *Indiplana oosora* gives no indication of such a bulb enclosing the male complex, although a reticulum of coarse parenchymatous fibres surround the ejaculatory duct and penis-papilla. This difference is here regarded as specific, not generic, and is discussed below.

Phylloplana lactea Laidlaw, 1903

Armatoplana lactea (Laidlaw) Faubel, 1983

LOCALITIES. On sand-flats and among coral fragments at low tide, west coast of Inhaca Island, Mozambique. (V. Gabie *leg.*) Also East African coast (Laidlaw, 1903).

DESCRIPTION (Fig.9). Six specimens from Mozambique in

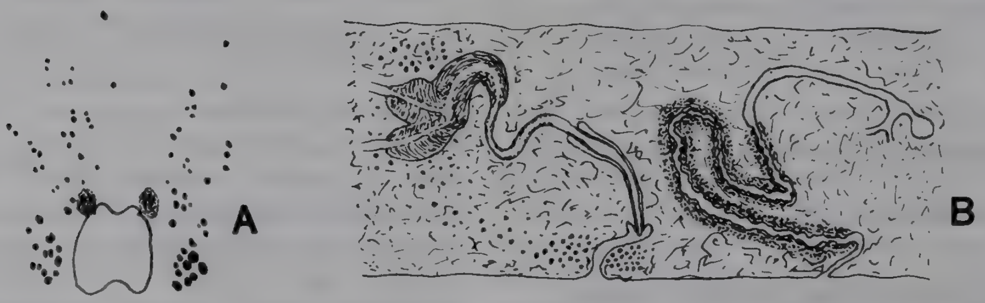

Fig.9 *Phylloplana lactea*: A, cerebral and tentacular eye-clusters; B, sagittal section of copulatory organs.

various stages of development are available for study. They measure 27–30 mm in length and 13–16 mm in maximum width. In life, the whitish body is profusely covered dorsally with small brownish spots forming a reticulate pattern, except along the margins and in the cerebral region. The median area of the mid-third of the body is dark brown, due to the underlying pharynx. On the postero-lateral borders of the cerebral organ lie two clusters of tentacular eyes, each cluster containing 11–18 eyes. Immediately anterior to these are smaller cerebral eyes arranged in two irregular rows, each with 27–34 eyes. Mouth more or less centrally situated; slender pharynx with several pairs of shallow lateral folds; intestinal trunk longer than pharyngeal chamber, bifurcating posteriorly, the two branches passing posteriorly round the copulatory complexes, whereas anteriorly the trunk trifurcates, the median branch passing dorsally to the cerebral organ. Many short lateral intestinal branches not anastomosing, each limb bifurcating near margin of body.

Mature specimens available agree very well with Laidlaw's description, but the male copulatory organs need some redescription. They lie immediately posterior to the pharynx and anterior to the male pore. Each vas deferens is convoluted, swollen and ending in a spermiducal bulb, which unites with the muscular proximal part of the ejaculatory duct to form a trilobed or anchor-shaped seminal vesicle. The central lobe of the vesicle extends antero-dorsally, narrows as it turns ventrally to continue as the ejaculatory duct leading into the base of a penis-papilla. In the present specimens, the penis-papilla is elongate and lies in a long penis-pocket opening into the male antrum through a broad but shallow penis-sheath. The papilla is coated with a cuticle for much of its length and when viewed ventrally very closely resembles the 'penis' depicted by Laidlaw. In not fully-mature specimens, however, there is a long narrow penis-papilla, but it does appear to be coated with a cuticle. No part of the male complex appears to be modified as a muscular or vesicular prostate. On the other hand, from the seminal vesicle much of the ejaculatory duct is lined with eosinophilic gland-cells, as found by Laidlaw. Also in agreement, the distal region of the ejaculatory duct is lined with cilia. Moreover, eosinophilic gland-cells occur in the parenchyma near the ventral wall of the seminal vesicle and are massed around the male antrum. Similar gland-cells occur dorsally to the union of the seminal vesicle and the ejaculatory duct. It seems likely that these gland-cells have a prostatic function, but their efferent ducts have not been made out in the material available. In a specimen with the male copulatory complex not fully developed such extracapsular gland-cells are not apparent and the lining of the ejaculatory duct shows no sign of producing an eosinophilic substance.

The female genital pore lies at about 1 mm posteriorly to the male. It leads into a narrow female antrum of variable length. From the antrum, a long vagina media, functioning as a 'shell'-chamber, is thrown into an anteriorly-directed loop—vagina media—reaching to about level with the male pore, where it turns to run posteriorly to a level dorsal to the female pore, where it opens into a vagina interna. The vagina media or 'shell'-chamber is therefore relatively long and provided with a thick coat of loose muscle-fibres invested with 'shell'- glands. Its lumen is narrow and somewhat corrugated. From the 'shell'-chamber, the vagina interna extends posteriorly for a short distance to receive the common duct of the uterine canals, following which the vagina terminates in a small bulbous Lang's vesicle. Uterine canals extend anteriorly to near cerebral organ, where they are not confluent.

SYSTEMATIC NOTE. *Phylloplana lactea* has been transferred by Faubel (1983) to a 'new' genus *Armatoplana*, with *Leptoplana panamensis* Plehn, 1896, as its type-species. The latter species is not congeneric with *P. lactea*, for it possesses an elongate muscular prostate and its seminal vesicle is not tripartite. A further species of *Phylloplana*, unnamed by Stummer-Traunfels (1933), but found by him among the original material of *Leptoplana purpurea* Schmarda, 1859, from Jamaica, has been placed by Faubel into a new genus, *Ilyella*, as *I. purpurea* (Stummer-Traunfels, 1933), but it undoubtedly belongs to the genus *Phylloplana*.

After examining the type-specimen of *Polycelis oosora* Schmarda, 1859, from Sri Lanka, Stummer-Traunfels (1933) erected the genus *Indiplana* for its reception, but Prudhoe (1985) gave reasons for regarding this genus as a synonym of *Phylloplana*. Faubel (1983), however, maintained *Indiplana* as a valid genus and placed it in the family Leptoplanidae, presumably because it possesses a 'male copulatory complex enclosed in massive muscular bulb', whereas he placed *Phylloplana* in the family 'Stylochoplanidae' which lack such a muscular bulb. A careful examination of Stummer-Traunfels description and figure of *Indiplana oosora* gives no indication of a 'massive muscular bulb', although he does describe a reticulum of parenchymatous fibres enclosing the male complex and in this respect resembles *Phylloplana tropicalis* (Hyman, 1954).

The main differences between *oosora* and *lactea* are the possession in the former of a reticulum of parenchyme-fibres investing much of the male complex, and a vagina media without a loose coating of muscle-fibres invested with 'shell'-glands. These differences are here regarded as being of specific value only, hence *Indiplana oosora* becomes *Phylloplana oosora* (Stummer-Traunfels, 1933) comb. nov.

Not fully-mature specimens in the present material offer an interesting point of value in the classification of polyclads, inasmuch as the male copulatory organs are initially formed without certain histological elements being apparent. For instance, eosinophilic gland-cells investing or lining the proximal region of the ejaculatory duct in mature specimens may not yet be developed in immature specimens, and the penis-papilla may not yet be covered with cuticle. The absence of these features might lead a student to regard a not fully-mature specimen to be taxonomically distinct from a fully-mature one. It seems, therefore, unwise to differentiate genera solely on the presence or absence of a penis-stylet, or of a supposed lack of certain gland-cells associated with the male reproductive system.

Genus ***HAPLOPLANA*** Laidlaw, 1903

DIAGNOSTIC FEATURES. Small, oval, rather stout forms without tentacles. Eyes in two elongate clusters alongside cerebral organ. Pharynx in anterior half of body; intestinal branches anastomosing. Genital pores more or less centrally situated. Apparently no seminal vesicle nor prostate present. Vasa deferentia lead into small vesicle (? penis-papilla) lying in small antrum. Vagina short; Lang's vesicle small; uterine canals not confluent anteriorly.

NOTE. Prudhoe (1985) discussed the problems arising from the inadequate description of this genus. Faubel (1983) placed *Haploplana elioti* in a new genus, *Euplanoida*, but Laidlaw's species appears not to have a seminal vesicle nor a coiled ejaculatory duct, said to be characteristic of *Euplanoida*.

Haploplana elioti Laidlaw, 1903

LOCALITY. British East Africa—probably Zanzibar.

DESCRIPTION. Laidlaw, 1903*a*: 109.

Genus *PULCHRIPLANA* Palombi, 1938

DIAGNOSTIC FEATURES. Oval forms with tentacles. Eyes at base of each tentacle, between which lie two small groups of cerebral eyes. Pharynx central; intestinal branches not anastomosing. Vasa deferentia arise in posterior region of body and anteriorly to open separately into small muscular seminal vesicle; prostate said not to be developed, but extracapsular eosinophilic gland-cells invest distal region of ejaculatory duct; penis-papilla very small. Female antrum spacious; large thin-walled vesicle opens into hind region of antrum. Vagina narrow, with small bursa between antrum and 'shell'-chamber; Lang's vesicle slender.

Pulchriplana insignis Palombi, 1938

LOCALITY. Reef Bay, Port Elizabeth, South Africa.

DESCRIPTION. Palombi, 1938: 342.

Subfamily STYLOCHOPLANINAE Meixner, 1907

DIAGNOSTIC FEATURE. Muscular prostate vesicular

Key to stylochoplanine genera from African waters

1	Epithelial lining of prostate with longitudinal tubes or radial folds	2
1′	Lining without such tubes or folds	3
2	Epithelial lining of prostate with deep radial folds	***Notoplanella***
2′	Epithelial lining of prostate with longitudinal tubes	***Notoplana***
3	Copulatory complexes very near hind end of body	***Zygantroplana***
3′	Copulatory complexes well separated from hind end of body	***Stylochoplana***

Genus *STYLOCHOPLANA* Stimpson, 1857

Notoplanides Palombi, 1928

DIAGNOSTIC FEATURES. Rather translucent forms, usually broadly rounded anteriorly and narrowing posteriorly. Nuchal tentacles may be present. Eyes in paired cerebral and tentacular groups or in two elongate clusters alongside cerebral organ. Seminal vesicle well developed; prostate rounded to elongate, with smooth epithelial lining; ejaculatory duct not projecting into lumen of latter; penis-papilla variably developed and may bear stylet. Vagina simple, with or without Lang's vesicle.

NOTE. Faubel (1983) has presented the genus *Stylochoplana* in a new sense and distributed its 40 or more species among 11 genera, 6 of which are said to be new. This re-organization contains so many doubtful premises that the present writer prefers to retain *Stylochoplana* Stimpson *sensu* Bock (1913) and its accompanying species. It is, however, admitted that *Stylochoplana* in the latter sense contains many species that require serious study of fully-mature specimens and an understanding of the changes that take place in the structure of the copulatory complexes during their development.

Key to *Stylochoplana* species from African waters

1	Penis-papilla with stylet	2
1′	Penis-papilla without stylet	5
2	With vagina bulbosa	***vesiculata***
2′	Without vagina bulbosa	3
3	Two lateral vesicles open into Lang's vesicle	***affinis***
3′	Without such vesicles	4
4	Genital pores near posterior margin of body	***robusta***
4′	Genital pores well separated from hind margin of body	***tenuis***
5	Without Lang's vesicle	6
5′	With Lang's vesicle	7
6	Dorsal surface with two broad submedian bands of brownish yellow	***inquilina***
6′	Dorsal surface without such bands	***simplex***
7	Thick-walled vagina externa	***suesensis***
7′	Thin-walled vagina externa	8
8	Cup-shaped depression between genital pores	***genicotyla***
8′	Without such a depression	9
9	Body narrowly elongate	***graffii***
9′	Body oval or cuneate	10
10	With common genital pore	***agilis***
10′	Genital pores separated	11
11	Genital pores widely separated	***modesta***
11′	Genital pores near each other	12
12	Eyes in two elongate clusters	***parva***
12′	Eyes in four separate clusters	13
13	Lang's vesicle elongate	***nadiae***
13′	Lang's vesicle crescentic	***capensis***

Stylochoplana affinis Palombi, 1940

LOCALITY. In *Teredo* tube among mangroves at Banana, Zaire.

DESCRIPTION. Palombi, 1940: 117.

DIAGNOSTIC FEATURES. Oval body 6 mm long and 3.5 mm wide. Dorsal surface yellowish, tinted with chestnut brown to near margins. No tentacles. Eyes in paired cerebral and tentacular clusters, latter alongside cerebral organ, former immediately anterior to larger tentacular eyes. Genital pores well separated from hind margin of body. Seminal vesicle pyriform, arcuate; relatively large prostate pyriform; penis-papilla very small, with long stylet in penis-pocket; penis-sheath distinct. Pair of rounded vesicles lateral to Lang's vesicle, with which they communicate.

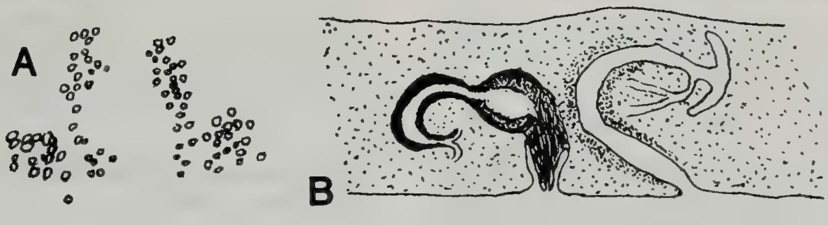

Fig.10 *Stylochplana capensis*: A, cerebral and tentacular eye-clusters; B, sagittal section of copulatory organs.

Stylochoplana agilis Lang, 1884

LOCALITIES. Akari, Ocean, Bouznika, Sidi R'bat, Atlantic coast of Morocco (G. Bitar *leg.*) Also known from the English Channel, Portugal and the western Mediterranean.

DESCRIPTIONS. Lang, 1884: 456; Prudhoe, 1982*a*: 46.

DIAGNOSTIC FEATURES. Cuneate body light brown dorsally with brown, red-brown or brownish black specks, absent in narrow whitish marginal band which sometimes bears violaceus streaks. Nuchal tentacles distinct. Cerebral eyes few, in two clusters lying between two groups of few eyes lying at bases of tentacles. Pharynx central. Common genital pore. Globular seminal vesicle opens directly into well-developed globular prostate; penis-papilla small, unarmed. Lang's vesicle small.

Stylochoplana capensis sp.nov.

LOCALITY. Brede River, Cape Province, South Africa (from 'rocks outside estuary mouth proper'), 7.7.1951. B.M.reg.no. 1987.3.11.4.

DESCRIPTION (Fig.10). The only specimen available is oval in outline, 10 mm in length and 4 mm in maximum width, being narrower anteriorly than posteriorly. Without tentacles. Eyes in separate paired cerebral and tentacular clusters. Mouth central; pharynx with seven pairs of shallow lateral folds in mid-third of body.

Genital pores close together. Male copulatory complex closely posterior to pharynx. Vasa deferentia arise laterally to pharynx and extend posteriorly to converge towards median line where they unite and immediately open into ventrally-disposed proximal end of an arcuate seminal vesicle. Through a very short ejaculatory duct, the seminal vesicle opens into a globular prostate, lined with a low epithelium. From the prostate, the ejaculatory duct passes into a thick, conical, unarmed penis-papilla occupying the entire male antrum.

The vagina is thrown into a loop dorsal to the penis-papilla. A shallow female antrum leads into a well-developed 'shell'-chamber which extends to the point in the loop where the vagina turns posteriorly to continue as the vagina interna. Shortly after the union of the 'shell'-chamber and the vagina interna, the latter receives the common uterine duct shortly before opening into a somewhat crescentic Lang's vesicle, with its limbs directed anteriorly and lined with low epithelium. After leaving the common uterine duct the two uterine canals each bifurcate, the inner limbs containing mature ova and extending anteriorly to become confluent in the median line between the eye-clusters and the pharynx, whereas the outer limbs appear empty and extend in the ventral parenchyma, but very soon pass into the dorsal parenchyma to reach the pharynx.

NOTE. The new form may be distinguished from known species of the genus *Stylochoplana* by the presence of a somewhat crescentic Lang's vesicle and a bifurcation of each uterine canal—an unusual feature already recorded by Kato (1934) in *Stylochoplana pusilla* Bock, 1924, which may be separated from the new form by the presence of nuchal tentacles, a male copulatory complex placed some distance posteriorly to the pharynx, a pyriform prostate and a large bulbous Lang's vesicle.

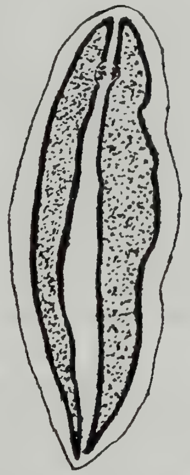

Fig.11 *Stylochoplana inquilina*, dorsal surface of body.

Stylochoplana genicotyla Palombi, 1939

LOCALITY. Baie de Caballo, Rio de Oro (24°13'N, 15°44'W), West Africa, 2.11.1938.

DESCRIPTION. Palombi, 1939*b*: 101.

Stylochoplana graffii (Laidlaw, 1906) Bock, 1913

Leptoplana graffii Laidlaw, 1906

LOCALITY. Among nodules of nullipores dredged in 27 to 55 metres, Cape Verde Is.

DESCRIPTION. Laidlaw, 1906: 708.

DIAGNOSTIC FEATURES. Body pallid, with broad, sandy-coloured longitudinal median band with ramifying branches, elongate and measuring 25 mm long and 3.5 mm wide. Eyes in two tentacular groups lateral to cerebral organ, each group with 4 or 5 large eyes; anteriorly to, but distinctly separated from, each group are 7 or 8 smaller cerebral eyes. Pharynx in anterior half of body. Genital pores separated, anteriorly placed. Seminal vesicle small, opens into prostate without interposition of ejaculatory duct. Prostate relatively large, pyriform and highly muscular and lined with smooth shallow epithelium. Seminal vesicle and prostate bound together by a common musculature. Penis-papilla stout, without stylet. Lang's vesicle large.

Stylochoplana inquilina Hyman, 1950

LOCALITY. Associating with anemone *Calliactis* opposite Sacco coral reef, Inhaca I., Mozambique.

DESCRIPTION. Hyman, 1950: 55.

DIAGNOSTIC FEATURES (Fig.11). Body lanceolate, up to 25 mm in length and 7 mm in maximum width. Dorsal surface white or pinkish with two broad submedian bands of brownish yellow edged with a narrow band of dark brown, each band tapers towards its extremities. No tentacles. Eyes in paired cerebral and tentacular clusters; former, with about 50 eyes in each cluster, latter with about 40 eyes. Pharynx narrow, extending through third and fourth fifths of body. Genital pores closely separated. Vasa deferentia open separately into antero-ventral region of oval muscular seminal vesicle; short ejaculatory duct unites seminal vesicle with large bulbous prostate. Conical penis-papilla without stylet. Vagina externa large; no Lang's vesicle.

NOTE. No specimen is available for study, but a water-coloured painting (Fig.11) of it leaves no doubt as to its identity. The Inhaca specimen was originally identified by Miss Hyman. This species was originally reported from Hawaii, where it was found at a depth of about 30 metres inhabiting the umbilicus in the shell of a *Tonna* snail, occupied by a hermit-crab, and to which the anemone *Calliactis armillata* was attached. The colour-pattern of the polyclad harmonized with that of the shell and the anemone.

Stylochoplana modesta (Quatrefages 1845) comb.nov.

Polycelis modesta Quatrefages, 1845
Leptoplana pallida (Quatref.) Laidlaw, 1906
Stylochoplana pallida (Quatref.) Palombi, 1928

LOCALITIES. From encrustations on rocks exposed to surf at Port Sal Rei, Boa Vista, Cape Verde Is (Laidlaw), and immature specimen from Lake Timsah, Suez Canal (Palombi). Originally found in the Bay of Naples.

DESCRIPTIONS. Quatrefages, 1845:133; Lang, 1884:489.

NOTE. It seems that Lang (1884) has confused *Polycelis pallidus* Quatrefages, 1845, and *Polycelis modestus* Quatrefages, 1845, and regarded them as varieties of the same species, *Leptoplana pallida*. It is clear from Quatrefages' figures that the two species are specifically distinct from each other in at least three features. Firstly, in *pallidus* the pharynx lies in the middle region of the body, whereas in *modestus* it lies in the anterior half; secondly, in *pallidus* the vasa deferentia open separately into a bulbous seminal vesicle, which lies well anteriorly to a broadly pyriform prostate, whereas in *modestus* the vasa deferentia unite to enter a fusiform seminal vesicle lying ventrally to a comparatively large pyriform prostate; and thirdly, in *pallidus* the very small penis-papilla bears a long slender stylet, absent in *modestus*. A close comparasion of the original descriptions and figures of these two species reveals other differences between them. Again, it seems that Lang's description of *Leptoplana pallida* is based on that of *Polycelis modesta*, so it is reasonable to assume that the records of *pallida* by Laidlaw (1906) and Palombi (1928) are really those of *modestus*. It needs to be noted that Faubel (1983) transferred *Stylochoplana pallida* (Quatrefages) *sensu* Lang (1884), *S. gracilis* (Heath & McGregor) and *S. hancocki* Hyman to the genus *Emprosthopharynx* Bock, 1913. In their gross morphology, these species bear scarcely any resemblance to the type-species of *Emprosthopharynx*, *E. opisthoporus* Bock, and are here returned to the genus *Stylochoplana*.

Stylochoplana nadiae (Melouk, 1941) du B. R. Marcus & Marcus, 1968

Leptoplana nadiae Melouk, 1941

LOCALITY. Adhering to oral arms of a syphozoan in northern region of Red Sea.

DESCRIPTION. Melouk, 1941: 41.

DIAGNOSTIC FEATURES. Elongate-oval body up to 22 mm long and 7 mm wide. No tentacles. Two tentacular eye-clusters, each with 15–16 large eyes; between these clusters lie two cerebral clusters, each with a few smaller eyes. Mouth more or less centrally placed. Genital pores separated in middle of posterior half of body. Vasa deferentia open together into elongate arcuate seminal vesicle; pyriform prostate of moderate size; penis-papilla large and conical, nearly fills shallow male antrum. Female copulatory complex enclosed in thick musculature; 'shell'-chamber relatively long; Lang's vesicle elongate.

Stylochoplana parva Palombi, 1939

LOCALITY. Cap Blanco, Rio de Oro (24°15′N, 15°44′W), West Africa, 9.11.1935.

DESCRIPTION. Palombi, 1939*b*: 104.

DIAGNOSTIC FEATURES. Delicate oval body 12 mm long and 6.5 mm wide. Ground-colour yellow, median zone and marginal band of a more distinctive yellow, while the remainder of the dorsal surface is diffused with grey. No tentacles. Eyes in two elongate clusters lateral to cerebral organ; tentacular eyes in posterior region of each cluster. Pharynx mainly anterior to middle of body. Genital pores separated in third fifth of body. Vasa deferentia open together into robust seminal vesicle; prostate elongate, with thick musculature, ventral to seminal vesicle; small unarmed penis-papilla in shallow male antrum. Vagina simple, thrown into an anteriorly-directed loop, terminates in small Lang's vesicle. Two small vesicles attached to vagina at its union with Lang's vesicle.

Stylochoplana robusta (Palombi, 1928) du B. R. Marcus & Marcus, 1968

Notoplana robusta Palombi, 1928

LOCALITY. Kabrit, Suez Canal, 21.10.1924.

DESCRIPTION. Palombi, 1928, 596.

DIAGNOSTIC FEATURES. Oval body fleshy, 3.5–6.5 mm long and 2–4.5 mm wide; dorsal surface chestnut brown. Tentacles absent. 6–8 tentacular eyes on each side of cerebral organ; cerebral eyes smaller, in two elongate clusters mainly anterior to tentacular eyes. Mouth central. Genital pores well separated in hind region of body. Vasa deferentia unite before opening into well-developed globular seminal vesicle; prostate pyriform, posterior to seminal vesicle; small penis-papilla bearing moderately long stylet in penis-pocket. Vagina externa thin walled; Lang's vesicle small.

Stylochoplana simplex **sp.nov.**

Localities. Cape Province, South Africa. Among rock in 3–4 metres below LWST., Windmill Beach, False Bay (*Holotype*. B.M.reg.no. 1987.3.17.46); on rocks off Rooi Els in 16–19 metres, False Bay, 29.7.52: on rock in 12–14 metres, Roman Rock, False Bay, 23.9.54; on rock in 4–6 metres below LWST, Oakland Pt., False Bay; intertidal in cochlear zone, Froggy Pond, 28.8.54.

Description (Fig.12). Delicate elongate forms said to be 'white and frilly' when active, measuring up to 9 mm long and 3 mm wide. Eyes disposed in two elongate groups alongside cerebral organ; cerebral eyes anterior to larger tentacular eyes in each cluster. Pharynx has shallow marginal folds in mid-third of body. Genital pores widely separated. Male copulatory complex immediately posterior to pharynx. Vasa deferentia unite to open into proximal end of fusiform seminal vesicle directed antero-dorsally. Ejaculatory duct short, directed posteriorly from seminal vesicle to open into an elongate-oval prostate lined with a shallow epithelium. The prostate opens directly into a relatively large, conical, unarmed penis-papilla lying in a relatively deep male antrum. Vagina narrow and thrown into a long anteriorly-directed loop, but not reaching the male complex. Vagina externa short; 'shell'-chamber long; vagina interna short, into the proximal end of which open the uterine canals. The features of *S. simplex* are the very simple copulatory complexes, the widely-separated genital pores, the elongate prostate and the absence of Lang's vesicle.

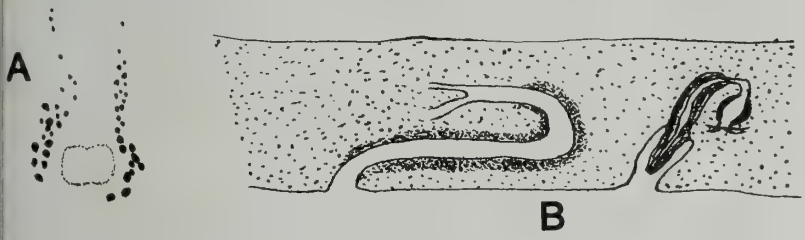

Fig.12 *Stylochoplana simplex*: A, tentacular and cerebral eye-clusters; B, sagittal section of copulatory organs.

Stylochoplana suesensis **Palombi, 1939**

Stylochoplana angusta Palombi, 1928, *nec* Verrill, 1893
Notoplanides opisthopharynx Palombi, 1928
Stylochoplana opisthopharynx (Palombi) Faubel, 1983

Localities. Ferry Port, Suez Canal, 28.11.1924; dredged at Toussoum, Suez Canal, 29.11.1924.

Description. Palombi, 1928: 590, 599.

Diagnostic features. Delicate body brownish, somewhat darker dorsally; about 8 mm long and up to 3 mm wide. No tentacles. Eyes in two elongate clusters alongside cerebral organ. Pharynx posterior to middle of body. Separated genital pores in posterior region of body. Vasa deferentia may open together into seminal vesicle or by a short duct. Short ejaculatory duct unites seminal vesicle with pyriform prostate. Penis-papilla very small, unarmed. Vagina externa muscular; Lang's vesicle small.

Note. Palombi (1928) erected the genus *Notoplanides* with *opisthopharynx* as its type-species. This species was erected on a damaged and badly contracted specimen. The proposed new genus is based on the very close proximity of the genital pores to the posterior margin of the body. But, as Palombi states, in the single specimen available to him, a portion of the hind region of the body is missing, so that the actual relationship of the genital pores to the posterior margin of the body in a complete specimen is not known.

Palombi also includes in *Notoplanides* an immature leptoplanid partially described by Bock (1923), from Easter Island, because of the posterior position of its pharynx. Palombi did not seem to realize that in young leptoplanids the pharynx tends to assume a posterior position, but with the development of the copulatory organs posteriorly to the pharynx the hind region of the body lengthens and the pharynx thereby moves to a more central position. On the other hand, du Bois-Reymond Marcus and Marcus (1968) have described *Notoplanides alcha* which has both pharynx and copulatory organs in hind third of body-length, but Faubel (1983) has transferred this species to *Stylochoplana* and this move is here accepted, because all gradations in the position of the pharynx between the anterior third and the posterior region of the body are to be found among species of this genus.

Stylochoplana tenuis **Palombi, 1936**

Localities. South Africa. Cape Province (sublittoral fringe, Oakland Pt, False Bay, 12–10.54; intertidal cochlear zone, Oakland Pt., 12.10.54.). Natal (from hull of ship permanently moored at Salisbury Island, Durban Bay, 15.1.51; scraped from buoy at junction of Maydon and Congella Channels, Durban Bay, 24.4.52). Also known from Still Bay, Cape Town (Palombi, 1936), and from Shelley Beach, East London (Palombi, 1939).

Description. Palombi, 1936:13, 1939*a*:126.

Diagnostic features (Fig.13). Body rounded anteriorly, narrowing posteriorly, 5–17 mm long and 3–8 mm wide. Dorsal surface brownish or yellow-ochre, weakly tinged with grey, sometimes with a marginal reticulum of greyish. Without tentacles. Eyes in two elongate clusters alongside cerebral organ, larger tentacular eyes in hind region of each cluster. Pharynx more or less central. Genital pores approximate, and well separated from hind margin of body. Vasa deferentia open into proximal end of thick-walled seminal vesicle; latter elongate oval, curves antero-dorsally to open directly into elongate-oval or fusiform prostate with thick walls and lined with a smooth glandular epithelium; prostatic duct tortuous and opening into small penis-papilla coated with a cuticle and lying in a penis-pocket; penis-sheath present. Anteriorly looped thin-walled vagina reaches the male complex. Lang's vesicle bulbous.

Note. The terminal portion of the male copulatory complex as described by Palombi does not seem to agree well with his figure of a sagittal view of the complex. The penis-papilla is described as small, conical, without a stylet, but in his figure it appears as a large amorphous mass filling much of the male antrum. The complex is also said to be without a penis-pocket, but in the same figure there is a suggestion that such a pocket does occur.

The present specimens from South Africa agree well with Palombi's species from Still Bay, differing in the presence of a penis-pocket. The penis-papilla is exactly like the short, slender conical structure seemingly lying in a penis-pocket depicted by Palombi, but in the present specimens the papilla is covered with cuticle. It is, therefore, here considered that

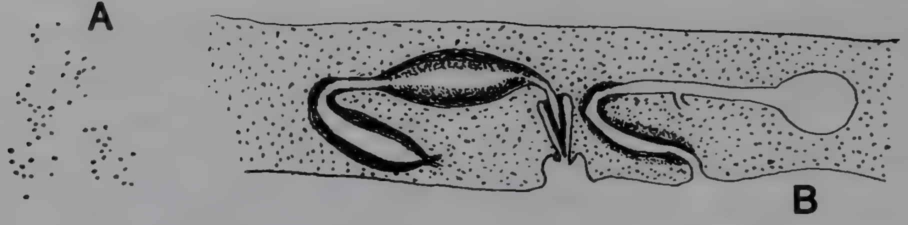

Fig.13 *Stylochoplana tenuis*: A, tentacular and cerebral eye-clusters; B, sagittal section of copulatory organs.

Stylochoplana tenuis possesses a cuticle-covered penis-papilla lying in a penis-pocket.

Stylochoplana vesiculata Palombi, 1940

LOCALITIES. On reef covered with algae at Cabinda, Angola (Palombi) and among littoral rocks at Mocamedes, Praia das Conchas, Angola, 18.10.1949 (de Beauchamp).

DESCRIPTIONS. Palombi, 1940:113; de Beauchamp, 1951:75.

DIAGNOSTIC FEATURES. Body rounded oval, 10–16 mm in length and 6–8 mm in width. Yellowish dorsally, ash-grey ventrally. Tentacles retractile. Cerebral eyes in two elongate clusters, each with about 50 eyes, dense in each group anteriorly, decreasing in number posteriorly; tentacular eyes in two groups, each with about 40 eyes, laterally to cerebral eyes. Pharynx central. Genital pores separated at about four-fifth level of body length. Muscular seminal vesicle small, opens directly into well-developed pyriform prostate; small penis-papilla with stylet lying in penis-pocket. Vagina externa with thick muscular walls. Lang's vesicle large and pyriform; on side of narrow region of the vesicle there is a vesicular appendage, which suggests that Lang's vesicle might be horseshoe-shaped or crescentic later in its development.

Genus *NOTOPLANA* Laidlaw, 1903

DIAGNOSTIC FEATURES. Body more or less oval, sometimes cuneate. Short contractile tentacles may occur. Eyes in paired cerebral and tentacular clusters, which may be distinctly separated into four groups, or merged into two elongate clusters, the larger eyes in each cluster being tentacular. Pharynx central. Genital pores separated. Seminal vesicle well developed; ejaculatory duct projecting well into lumen of bulbous prostate lined with a tall epithelium containing longitudinal tubes lying parallel to duct; penis-papilla of variable development, sometimes covered with a cuticle or bearing a thin stylet. Vagina thrown into any anteriorly-directed loop; Lang's vesicle may be present.

Key to *Notoplana* species from African waters

1	Penis-papilla without stylet or cuticular covering	2
1′	Penis-papilla with stylet or tipped with cuticle	3
2	Eyes in two elongate clusters	***gardineri***
2′	Eyes in four distinctly separated clusters	***patellarum***
3	Long penis-stylet in penis-pocket	4
3′	Penis-papilla large, tipped with cuticle; no penis-pocket	***alcinoi***
4	Sucker between genital pores	***cotylifera***
4′	No genital sucker	5
5	Lang's vesicle small	***vitrea***
5′	Lang's vesicle large and elongate	6
6	Vagina externa thin walled	***atlantica***
6′	Vagina externa very muscular	***atomata***

Notoplana alcinoi (Schmidt, 1861) Bock, 1913

Leptoplana alcinoi Schmidt, 1861
Notoplana igiliensis Galleni, 1974

LOCALITIES. Among nodules of nullipore in 9 to 18 metres. St Vincent Harbour, Cape Verde Is (Laidlaw, 1906); several localities along Moroccan coast (G. Bitar *leg.*) Apparently common in Mediterranean waters from the Iberian Peninsula to the Black Sea.

DIAGNOSTIC FEATURES. Body up to 20 mm in length, dorsal surface with brownish, yellow-brown, dark brown or greyish spots. Tentacles as shallow bosses, not always apparent. Eyes in two elongate groups, smaller cerebral eyes mostly anterior in each group, larger tentacular eyes posterior. Genital pores approximate in hind quarter of body. Seminal vesicle smaller than prostate; deep epithelial lining of prostate with 5–7, usually 6, longitudinal chambers. Large, elongate, conical penis-papilla muscular, tipped with cuticle. Vagina bulbosa developed; Lang's vesicle small.

NOTE. Galleni (1974) recognized the very close resemblance between *alcinoi* and his *igiliensis*, but differentiates the species only on size, on an arbitary difference in the relative position of the cerebral and tentacular eye-clusters and on the union of the uterine canals anteriorly to the pharynx in *alcinoi* and their separation in *igiliensis*. The first two of these differences have no sound taxonomic value, and the third difference is no doubt due to specimens of *igiliensis* not being fully gravid, because among many leptoplanid genera the anterior confluence of the uterine canals does not appear until full development of the female complex is attained.

Notoplana atlantica Bock, 1913

Leptoplana nationalis Plehn, 1896

LOCALITY. Trawled at 120 metres, 8°S. 14.5°W., near Ascension I., Atlantic Ocean.

DESCRIPTION. Plehn, 1896*b*:6.

DIAGNOSTIC FEATURES. Delicate whitish worm, 9 mm long. Eyes in two elongate groups with 20–23 eyes in each group; larger tentacular eyes posterior to cerebral eyes in each group. Mouth central. Genital pores approximate, at about junction of middle and hind thirds of body. Vasa deferentia open independently into globular seminal vesicle; large globular prostate dorsal to seminal vesicle. Epithelial lining of prostate contains usual longitudinal chambers. Penis-papilla small, but tipped with a long stylet in a long penis-pocket.

Vagina spacious, thin walled; 'shell'-chamber long and narrow; Lang's vesicle elongate.

Notoplana atomata (Müller, 1776) Bock, 1913

Planaria atomata Müller, 1776
Leptoplana atomata Johnston, 1865

LOCALITY. Port Said, Egypt, 15.12.1924 (Palombi, 1928).

DESCRIPTIONS. Bock, 1913:195; Hyman, 1939*b*:135.

DIAGNOSTIC FEATURES. Body may be oval or somewhat cuneate, up to 28 mm long and 13 mm wide; dorsal surface white or covered with various shades of brown, spotted with reddish brown or reddish brown with dark spots. No tentacles. Cerebral eyes in two elongate clusters extending anteriorly from cerebral organ; larger tentacular eyes in two clusters lateral to hind end of cerebral clusters. Mouth central. Genital pores separated. Vasa deferentia open separately into an arcuate or bulbous seminal vesicle. Prostate posterior to seminal vesicle, with epithelial lining containing 6 or 7 longitudinal chambers. Penis-papilla small, bearing a long stylet lying in a long penis-pocket. Vagina externa long and strongly muscular; Lang's vesicle elongate.

NOTE. There appears to be some uncertainty as to the accuracy of Palombi's determination of specimens from Port Said as *N. atomata*. This species ranges from Scandinavia to the English Channel and in the boreal regions of the Atlantic and Pacific coasts of North America. Delle Chiaje (1831 and 1841) provisionally identified specimens from Naples and Sicily as *Planaria atomata* Müller, but he expressed some doubt about his identification, as well as the occurrence of this species in the Mediterranean. It is, however, not possible to recognize delle Chiaje's specimens as *N. atomata* from his description. It seems, therefore, that the occurrence of this species at the Mediterranean entrance to the Suez Canal must at present be considered doubtful, especially as Palombi gave no description of his specimens. His specific determination does, however, imply that his specimens possess a long penis-stylet and the close relative of *N. atomata* possessing such a stylet and occurring in the Mediterranean is *Notoplana vitrea* (Lang). Hence, it is possible that Palombi's specimens and those of della Chiaje belong to this species, which, for this reason, is here included as a probable African form.

Notoplana vitrea (Lang, 1884) Bock, 1913

Leptoplana vitrea Lang, 1884

LOCALITY. Mediterranean Sea.

DESCRIPTION. Lang, 1884:493.

DIAGNOSTIC FEATURES. Body delicate, cuneate, up to 40 mm long and 10 mm wide. Eyes in two elongate clusters, numerous cerebral eyes on either side of cerebral organ, larger tentacular eyes a little posterior and lateral to cerebral eyes. Mouth central. Genital pores near each other at about junction of middle and hind third of body and between them the musculature of the body-wall is thickened and the body-surface corrugated. Vasa deferentia open together into muscular arcuate seminal vesicle. Prostate well developed. From prostate, ejaculatory duct runs dorsally to open into small penis-papilla bearing long stylet in long penis-pocket. Distal portion of ejaculatory duct and penis-pocket enclosed in a thick muscular sheath. Vagina externa with thick muscular wall; Lang's vesicle small.

NOTE. The features distinguishing *N. vitrea* from *N. atomata* are the thickening and corrugation of body-wall between genital pores, the long duct connecting prostate with penis-papilla and the small Lang's vesicle.

Notoplana cotylifera Meixner,1907

LOCALITIES. Eylath, Gulf of Aqaba (H. Steinitz *leg.*) Also recorded from Gulf of Tadjourrah, Djibouti (Meixner, 1907) and in sponge associated with coral at Graa, Red Sea (Prudhoe, 1952). A specimen from Caesarea on Mediterranean coast of Israel has been determined by the writer as *N. cotylifera*.

DESCRIPTION. Meixner, 1907:448.

DIAGNOSTIC FEATURES. Body elongate oval, yellowish green and up to 24 mm long and 10 mm wide. Tentacles may be conical, with eyes at bases. Cerebral eyes in two elongate clusters between tentacles. Mouth in mid-third of body; pharynx short. Genital pores well separated, closely posterior to pharynx. Genital sucker between pores. Vasa deferentia open separately into seminal vesicle with thick musculature and narrow lumen. Prostate posterior to seminal vesicle, its tall epithelial lining containing 7 long tubes. Penis-papilla well developed, lined with a cuticle so that when the papilla is protracted it is covered with a cuticle. Male antrum spacious. Vagina externa short, 'shell'-chamber long; no Lang's vesicle.

NOTE. Meixner (1907) described and figured an anteriorly-directed pocket or a 'Rudiment einer accessorische Blase' in the middle of the vagina externa ('Eiergang'). The present specimens from the Gulf of Aqaba possess an accessory vesicle, but it arises from the anterior wall of the female antrum. Initially, this vesicle in lined with a tall epithelium, but its inner half appears to be merely a cavity in the parenchyme and without a recognizable lining. This cavity opens on the dorsal surface of the body, almost directly above the sucker lying between the genital pores. The dorsal aperture of this cavity is plugged with parenchymatous tissue. In the specimen from Caesarea there likewise appears to be an anteriorly-directed canal connected with the female antrum, but the cavity in the parenchyme is not yet developed, although the parenchyme in this region is exceptionally loose and could readily break down to form an ill-defined cavity.

Notoplana patellarum (Stimpson, 1855) Palombi, 1939

Leptoplana patellarum Stimpson, 1855
Polycelis lyrosora Schmarda, 1859
Polycelis erythrotaenia Schmarda, 1859
Leptoplana patellensis Collingwood, 1876
Notoplana ovalis Bock, 1913
Notoplana erythrotaenia Stummer-Traunfels, 1933
Notocomplana erythrotaenia Faubel, 1983

LOCALITIES. Cape Province, South Africa (Steenberg, 21.2.1939; in 3–8 metres below LWST., Glencairn Rocks, False Bay, 17.2.1953; intertidal, St. James, 1.9.1956; on rocks 'from LWST to 1 ft. higher', Oatland Pt, False Bay, 20.9.1954; low tide level on rock at mouth of Breede River Estuary, 5.7.1951. Usually found on rocks, or living between mantle and foot of *Patella*, particularly *P. oculus*; common along coast of Cape Province from Table Bay eastwards to East London (Stimpson,1855:389; Schmarda, 1859:24; Collingwood, 1876:93; Palombi, 1936:18 and 1939*a*:128). Has also been found in Mauritius, Indian Ocean (Bock, 1913:212).

DESCRIPTIONS. Bock, 1913:212; Palombi, 1939*a*:128.

DIAGNOSTIC FEATURES. Fleshy broadly-oval body, up to 17 mm long and 10.5 mm wide. Dorsal surface in varying shades of yellow with a wide brown or reddish central band; ventral surface greyish yellow. Tentacles may not be apparent or appear as shallow protuberances or bosses. Eyes in two separate cerebral groups and two tentacular groups. Mouth central; pharynx 4–5 mm long with 5 to 7 pairs of lateral folds. Genital pores in middle of hind third of body. Vasa deferentia unite to open into dorso-ventrally arcuate muscular seminal vesicle. Prostate posterior to seminal vesicle; its epithelium contains 8 longitudinal chambers. Penis-papilla robust, filling male antrum provided with tall glandular epithelial lining. Female antrum short and narrow; 'shell'-chamber long and narrow. Lang's vesicle small.

NOTE. Faubel (1983) erected the genus *Notocomplana* with *Leptoplana humilis* Stimpson, 1857, as its type-species and listed *Notoplana erythrotaenia* Stummer-Traunfels, 1933, = *N. patellarum* among its species. Included in the list are *N. evelinae* (Marcus, 1947), the type-species of the genus *Pucelis* Marcus, 1947, and *N. litoricola* (Heath & McGregor, 1913), the type-species of the genus *Freemania* Hyman, 1953. If the two latter species be accepted as congeners of *N. humilis*, then the name *Notocomplana* has no validity, according to Article 23 of the International Code of Zoological Nomenclature.

Notoplana gardineri (Laidlaw, 1904) Bock, 1913

Leptoplana gardineri Laidlaw, 1904

LOCALITY. Under rock near low-tide mark at Sherm Sheik, Red Sea (Prudhoe, 1952); also record from Sri Lanka (Laidlaw, 1904).

DESCRIPTIONS. Laidlaw, 1904:133; Prudhoe, 1952:176.

DIAGNOSTIC FEATURES. Body oval, yellowish white, somewhat pellucid; 16 mm in length and 7.5–9 mm in maximum width. Without tentacles. Eyes in two elongate clusters, smaller cerebral eyes anterior, larger tentacular eyes posterior. Pharynx central, much folded laterally. 4.5 mm long. Genital pores closely separated. Vasa deferentia unite to open into muscular arcuate seminal vesicle. Prostate elongate, dorsal and posterior to seminal vesicle; its tall glandular lining with 7 longitudinal chambers. From the prostate, the ejaculatory duct passes through a thick muscular sheath to enter a small unarmed penis-papilla lying in shallow male antrum. Female copulatory system has not yet been fully described, but does include a small Lang's vesicle.

Genus *NOTOPLANELLA* Bock, 1913

DIAGNOSTIC FEATURES. Body without tentacles. Eyes in two elongate clusters alongside cerebral organ. Pharynx in mid-third of body. Arcuate seminal vesicle linked with prostate by a short ejaculatory duct. Prostate large, elongate-oval, dorsal to seminal vesicle and lined with a deep epithelium thrown into radial folds; penis-papilla shallow. Vagina weakly developed, without Lang's vesicle.

NOTE. Faubel (1983) has placed *Notoplanella* in the family Cryptocelididae, but it is difficult to understand the reason for this action, except that it may have been induced by the fact that the epithelial lining of the prostate is thrown into radial folds. However, the gross morphology of *Notoplanella* is typically that of the leptoplanids.

Notoplanella inarmata Bock, 1931

LOCALITIES. Cape Province, South Africa (dredged in 19 metres, 34°12.9′S. 18°49.1′E., 16.2.65; Danger Point, 5.7.1939; Saldanha Bay, 27.4.1964; Langebaan, Saldanha Bay, 28.4.1949 and 8.5.1953). Also Simon's Bay, near Cape Town (Bock, 1931:272).

DESCRIPTION. Bock, 1931: 272.

NOTE. The fully mature specimen available to the writer agrees well with Bock's description of *N. inarmata*. There is a considerable thickening of the musculature of the body-wall around the genital pores, especially the female, and might give the female antrum the appearance of being a vagina bulbosa. This feature is little developed in a younger specimen.

Genus *ZYGANTROPLANA* Laidlaw, 1906

DIAGNOSTIC FEATURES. Elongate to elongate-oval forms without tentacles. Eyes in paired cerebral and tentacular groups or in two elongate clusters alongside the cerebral organ. Pharynx mainly posterior to middle of body. Copulatory complexes open into a common atrium or closely associated genital pores adjacent to posterior margin of body. Male and female copulatory complexes directed anteriorly from their respective openings, the male lying ventrally to female. Seminal vesicle moderately developed; prostate lined with smooth shallow epithelium; penis-papilla small. Vagina long, dorsal to male organs and terminating in a large Lang's vesicle. Uterine canals short.

Zygantroplana verrilli Laidlaw, 1906

LOCALITY. Among weeds in St Vincent Harbour, Cape Verde Is (Laidlaw, 1906).

DESCRIPTION. Laidlaw, 1906:709.

Family **GNESIOCEROTIDAE** Marcus & Marcus, 1966, emend. Prudhoe, 1982

DIAGNOSTIC FEATURES. Elongate-oval forms. Eyes in two elongate clusters alongside cerebral organ or in paired cerebral and tentacular clusters. Pharynx in mid-third of body or somewhat anterior, much folded marginally. Genital pores separated. Vasa deferentia may form a pair of spermiducal bulbs before opening into a true seminal vesicle or prostate. Prostate interpolated between sperm ducts or seminal vesicle and an eversible cirrus-sac. Cirrus-sac may contain a long cuticularized papilla or be lined with cuticle thrown into transverse ridges, but more often lined with bristles, spines or hooks; with thick musculature which may also invest the prostate. Vagina simple often with Lang's vesicle.

Key to gnesiocerotid genera from African waters

1 Ejaculatory papilla projecting into lumen of prostate 2
1′ Without papilla in prostate .... ***Gnesioceros***

2 Pyriform glandular organ in anterior wall of male antrum .... ***Neoplanocera***
2′ Without such an organ 3

3 Genital sucker with corrugated surface between genital pores .... ***Echinoplana***
3′ Highly glandular epithelium around genital pores .... ***Gabiella***

Genus *GNESIOCEROS* Diesing, 1861

DIAGNOSTIC FEATURES. Pellucid cuneate forms. Conical tentacles contain eyes; cerebral eyes in two scattered groups lateral to cerebral organ and between tentacles. Intestinal branches not anastomosing. Genital pores separated. Seminal vesicle well developed, opening directly into oval prostate lined with an epithelium thrown into deep radial folds. Conical cirrus lined with several transverse serrated ridges of cuticle. Vagina externa with wide glandulo-muscular fold invested with gland-cells. Lang's vesicle U-shaped or crescentic, limbs directed anteriorly.

Gnesioceros sargassicola (Mertens, 1832) *sensu* Graff (1892)

Planaria sargassicola Mertens, 1832
Stylochus pelagicus Moseley, 1877
Stylochoplana sargassicola Graff, 1892

LOCALITIES. Off West African coast (21°–35°N., 36°–38°W.) (Mertens, 1832); off West African coast (9°21′N., 18°25′W. and 5°48′N., 14°20′W.) (Moseley, 1877); West Africa and Madeira (Graff, 1892); dredged in about 2 metres at Boa Vista, Cape Verde Is (Laidlaw, 1906).

DESCRIPTIONS. Mertens, 1832:13; Moseley, 1877:24; Graff, 1892:207; Hyman, 1939*c*:11; du B.-R. Marcus & Marcus, 1968:48.

Genus *ECHINOPLANA* Haswell, 1907

DIAGNOSTIC FEATURES. Elongate forms without tentacles. Eyes in two elongate groups alongside cerebral organ. Pharynx mainly in anterior half of body; intestinal branches anastomosing. Genital sucker with corrugated surface between genital pores. Seminal vesicle elongate; prostate muscular and elongate, lined with smooth epithelium and joined with cirrus-sac by a convoluted ejaculatory duct invested with a mass of muscle-fibres. Very muscular cirrus-sac lined with spines. No male antrum. Vagina narrow, anteriorly directed from female pore , invested with 'shell'-glands in its inner and outer regions. Lang's vesicle rudimentary.

Echinoplana celerrima Haswell, 1907

LOCALITIES. Cape Province, South Africa (on vertical rock in 2–4 metres below LWST., Oakland Pt, False Bay, 10.6.1953; from mud under water at Hell's Gate, St Lucia Lakes, Saldanha Bay, 21.7.1949; among *Zostera* at tip of Point I. and from Charter's Creek, St Lucia Lakes, Saldanha Bay 5.7.1948.); Israel (Eylath, Gulf of Aqaba, Red Sea, May 1947, L. Fishelson & Cl. Lewinsohn *leg.*) This species appears to be widely distributed, having hitherto been recorded from southern Australia (Haswell, 1907; Prudhoe, 1982*b*) and from the Mediterranean Sea (Galleni, 1978).

DESCRIPTIONS. Haswell, 1907:475; Galleni, 1978:139; Prudhoe, 1982*b*:377.

Genus *GABIELLA* gen.nov.

DEFINITION. Gnesiocerotidae without tentacles. Eyes in two elongate clusters alongside cerebral organ. Pharynx with few lateral folds in mid-third of body. Genital pores separate, in depression lined with well-developed glandular epithelium in ventral wall of body. Seminal vesicle fusiform, ventro-dorsally disposed; ejaculatory duct opens through long papilla projecting into lumen of globular prostate lined with tall epithelium thrown into radial folds. Cirrus-sac lined with spines decreasing in size towards either end of sac. Prostate and cirrus-sac enclosed in weakly-developed musculature. Male antrum absent. Vagina thrown into an anteriorly-directed loop. Lang's vesicle small.

TYPE-SPECIES. *Gabiella inhacensis* gen.nov., sp.nov.

Gabiella inhacensis sp.nov.

LOCALITY. Among *Favia* opposite beacon on western shore, Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*) B.M.reg.no. 1985.7.3.1/2 syntypes.

DESCRIPTION (Fig.14). According to a water-coloured painting of the living worm, the body is light brown, with a darker brown median band. The body measures 9.7 to 12 mm long and a more or less uniform width of about 3 mm. Eyes in two elongate groups, each with 14 to 24 eyes, some of which are larger and more deeply pigmented than the remainder and represent tentacular eyes. Weakly-developed pharynx about 2 mm long.

Male and female genital pores situated at about midway between pharynx and posterior margin of body. Both lie in a depression of the body-wall lined with a wrinkled epithelium containing relatively large gland-cells. Vasa deferentia appear on either side of median line, near hind end of pharynx. They extend posteriorly as swollen convoluted canals to just anterior to the male pore, where they unite in the median line to form a very short common canal opening into the hind end or ventral wall of a seminal vesicle. This vesicle is thin-walled, somewhat fusiform with its long axis disposed dorso-ventrally against the anterior of the prostate. Dorsally a short ejaculatory duct runs posteriorly from the seminal vesicle to open into a ventrally-directed prostate through a long papilla projecting into its lumen. The prostate is oval, provided with a thick muscular wall and lined with a tall epithelium thrown into several deep radial folds. The prostate opens through a short duct into a narrow cirrus-sac lined with many spines of variable size, the larger spines occurring in the middle of the sac and gradually diminishing in size towards the proximal and distal ends of the sac. The latter opens directly to the exterior through the male pore, which lies at about 2.5 mm from the posterior margin of the body. The cirrus-sac and the prostate are enclosed in a feebly-developed muscular sheath. Male antrum not apparent. Vagina externa directed

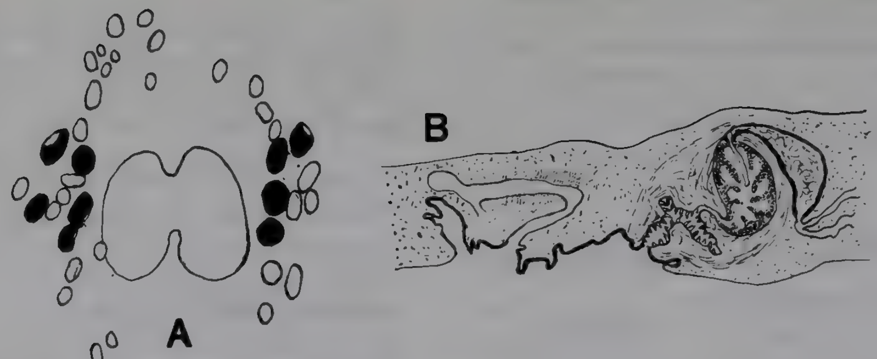

Fig.14 *Gabiella inhacensis*: A, cerebral and tentacular eye-clusters; B, sagittal section of copulatory organs.

antero-dorsally from female pore to near cirrus-sac, where it turns posteriorly to enter a narrow 'shell'-chamber. Throughout its length this chamber is surrounded by numerous 'shell'-glands. A little beyond the hind end of the 'shell'-chamber, the vagina receives the common duct of the uterine canals and, shortly beyond, the vagina ends in a small rounded Lang's vesicle. Vagina lined with a ciliated epithelium, whereas Lang's vesicle is lined with relatively large vacuolate cells. Uterine canals not anteriorly confluent.

NOTE. The above-described form bears a strong resemblance to *Echinoplana celerrima* Haswell, but differs in possessing a highly glandular epidermis around the genital pores, in the distribution of 'shell'-glands and in the presence of a long ejaculatory papilla projecting into the lumen of the prostate lined with a tall glandular epithelium thrown into deep radial folds. These differences appear to warrant the erection of a new genus here named *Gabiella* in honour of Dr Vivien Gabie, formerly of the Witwatersrand University, who has collected many interesting polyclads from the Mozambique Island of Inhaca.

Genus ***NEOPLANOCERA*** Yeri & Kaburaki, 1918

Cirroposthia Steinböck, 1937

DIAGNOSTIC FEATURES. Eyes in two elongate clusters. Body without tentacles. Pharynx in mid-third of body. Seminal vesicle elongate, thin-walled; elongate prostate lined with tall smooth epithelium and dorsal to seminal vesicle; cirrus-sac lined with spines or stiff bristles; prostate and cirrus-sac not enclosed in muscular sheath. Independent pyriform glandular organ lies ventrally to cirrus-sac and opens into male antrum. Vagina short and narrow. Lang's vesicle rudimentary or not apparent.

NOTE. Faubel (1983) stated that a 'true prostatic vesicle is lacking' in *Neoplanocera*, but he appears to have overlooked Kato's (1937) redescription of the type-species, *N. elongata*, in which it is shown that the genus possesses a distinct prostate. Moreover, Faubel also includes *Cirroposthia steueri* Steinböck in the genus *Neoplanocera* and in which Steinböck found a genuine interpolated prostate.

Neoplanocera steueri **(Steinböck, 1937) Marcus, 1947**

Cirroposthia steueri Steinböck, 1937

LOCALITY. Among algae in eastern harbour of Alexandria, Egypt (Steinböck). A specimen from Tel Aviv, Israel, was included in the collection sent to the writer for identification by Dr H. Steinitz.

NOTE. While the Israeli specimen is rather larger than that described by Steinböck, it otherwise agrees very well with the structure of the copulatory complexes of *N. steueri*.

Family **PLANOCERIDAE** Lang, 1884

DIAGNOSTIC FEATURES. Elongate to discoid forms, often with nuchal tentacles. Eyes in paired tentacular and cerebral clusters, or in two elongate groups at sides of cerebral organ. Pharynx central. Genital pores well separated from posterior margin of body. Male copulatory complex closely posterior to pharynx, anterior to male pore. Seminal vesicle or a pair spermiducal bulbs present. Prostate independent. Eversible cirrus-sac lined with spines. Vagina variably developed, sometimes with a muscular bursa, either as a vaginal bursa or a bursa copulatrix. Lang's vesicle variably developed.

Key to planocerid genera from African waters

1 Without nuchal tentacles; eyes in two elongate clusters .... ***Disparoplana***
1′ With nuchal tentacles; eyes in separated cerebral and tentacular clusters 2

2 With seminal vesicle; no spermiducal bulbs 3
2′ With spermiducal bulbs; no seminal vesicle .... ***Paraplanocera***

3 Eyes at base of tentacles.................... ***Planocera***
3′ Eyes within and at base of tentacles .... ***Planocerodes***

Genus ***PLANOCERA*** Blainville, 1828, *sensu* Lang (1884)

DIAGNOSTIC FEATURES. Large discoid or oval forms with slender nuchal tentacles. Eyes at base of tentacles; four ill-defined groups of cerebral eyes between tentacles. Pharynx with 4 to 6 pairs of deep lateral folds; intestinal trunk with 5 to 8 pairs of non-anastomosing lateral branches. Seminal vesicle strongly muscular; prostate bulbous and muscular with deeply folded epithelial lining; cirrus-sac lined with small spines, sometimes with one or more large spines or thorns at opening of sac into male antrum; ejaculatory duct and proximal region of cirrus-sac surrounded by a mass of loose connective tissue enclosed in a thick muscular sheath. Vagina bulbosa present. Lang's vesicle variable; uterine canals anteriorly separated.

Key to *Planocera* species from African waters

1 With one or more thorn-like hooks among small spines in cirrus-sac 2
1′ Cirrus-sac lined only with small spines 3

2 With one thorn-like hook .... ***pellucida***
2′ With three large thorn-like hooks on opening of cirrus-sac .... ***crosslandi***
2′ With several small thorn-like hooks on opening of cirrus-sac .... ***uncinata***

3 Vasa deferentia open into seminal vesicle by common canal .... ***graffii***
3′ Vasa deferentia open separately into seminal vesicle .... ***gilchristi***

Planocera crosslandi Laidlaw, 1903

Localities. Dredged in about 20 metres off mainland coast of East Africa (Laidlaw, 1903); associating with corsal, Sherm Sheik, Red Sea (Prudhoe, 1952).

Descriptions. Laidlaw, 1903*a*:100; Prudhoe, 1952:175.

Planocera gilchristi Jacubowa, 1906

Localities. Cape Province, South Africa (Quolora, 20.5.1939; Danger Point, 5.7.1939; among sand and loose weed in 1.5 to 1.8 metres in channel, Knysna Estuary, 16.7.1947; Great Brak River Estuary, 3.5.1950). Natal (Port Edward, 30.13.1938) (Day colln.). Fairly common, living under stones, but sometimes found creeping on exposed rock in pools, near Marine Laboratory, Cape Town, South Africa (Jacubowa, 1907). Still Bay, Cape Province 4.1.1932 (Palombi, 1936). Shelley and Bat's Cave Rocks, East London, Cape Province, 10–12.7.1937 (Palombi, 1939).

Descriptions. Jacubowa, 1908:145; Palombi, 1936:23, 1939*a*:129.

Planocera graffii Lang, 1879

Locality. Dredged in about 2 metres, Boa Vista, Cape Verde Is (Laidlaw, 1906:706).

Description. Lang, 1884:434.

Planocera pellucida (Mertens, 1832) Örsted, 1844

Planaria pellucida Mertens, 1832
Stylochus pelagicus Moseley, 1877

Localities. Atlantic Ocean 7°48′N. 23°56′W. (Mertens, 1832); off West African coast, 9°21′N. 18°25′W. and 5°48′N. 14°20′W. (Moseley, 1877); Cape of Good Hope, South Africa, and off north-east coast of Cape Verde Is (Graff, 1892.7.11); off Cape Town and Port Natal, South Africa (Bock, 1913); mid and South Atlantic and Red Sea (Faubel, 1983).

Descriptions. Graff, 1892:195; Bock, 1913:240; Moseley, 1877:24; Kato, 1938:231; Faubel, 1983:77.

Notes. Graff (1892:211) thought that Moseley may have described two species, *Planocera pellucida* and *Gnesioceros sargassicola*, under *Stylochus pelagicus*. The descriptions of this species by Graff (1892), Bock (1913) and Faubel (1983) do not mention the presence of a relatively large hooked spine at the connection of the cirrus-sac and the male antrum, as found by Kato (1938) and seen by the present writer in a North Sea specimen steeped in methyl salicylate for about 24 hours.

Planocera uncinata Palombi, 1939

Localities. Cape Province, South Africa: (Home Wood Beach, Port Elizabeth, 10.7.1936; Bat's Cave Rock, East London, 12.7.1937—Palombi, 1939,129); (The Haven, 9.1.1939 and from rocks, 2.4 km from mouth of Buchman's River Estuary, 10.9.1950—Day colln.)

Genus ***PLANOCERODES*** Palombi, 1936

Diagnostic features. Large broadly-oval forms with slender nuchal tentacles. Cerebral eyes in two irregular clusters between tentacular eyes within and at base of each tentacle. Intestinal branches not ramifying. Seminal vesicle small. Prostate large. Ductus communis prolonged into a large conical papilla covered with series of spines and lying in tubular spacious cirrus-sac. Female copulatory complex similar to that in *Planocera*.

Note. Palombi (1936) recognized the very close resemblance between *Planocerodes* and *Planocera*, but claimed that the former may be differentiated by the presence of eyes within and at the base of each tentacle and by the presence of a spiny penis-papilla. The difference in the disposition of the tentacular eyes is merely a specific feature, as found in the genus *Paraplanocera*, while the large conical spiny penis-papilla lying in the cirrus-sac of *Planocerodes ceratommata* is similar to the partially protracted inner region of the cirrus-sac sometimes found in *Planocera gilchristi*.

Planocerodes ceratommata Palombi, 1936

Locality. Still Bay, Cape Province, South Africa, 4.1.1932 (Palombi, 1936).

Description. Palombi, 1936:25.

Note. Faubel (1983) is probably justified in transferring this species to the genus *Planocera*, but for certainty it requires the careful re-examination and redescription of specimens of *Planocera gilchristi* in various stages of development. A paratype specimen of *P. ceratommata* has been examined by the present writer but it is in very poor condition.

Genus ***PARAPLANOCERA*** Laidlaw, 1903

Diagnostic features. Broadly-oval forms with slender nuchal tentacles. Eyes in paired tentacular and cerebral clusters. Pharynx with 4–7 pairs of deep lateral folds. Two spermiducal bulbs; no seminal vesicle; prostate bulbous, two chambered, with epithelium thrown into deep lateral folds. Cirrus-sac lined with spines. Short ejaculatory duct and much of the cirrus-sac in an intermuscular space filled with connective tissue; thick muscular sheath encloses prostate and cirrus-sac. One pair of glandular pockets open into male antrum. Posteriorly-directed bursa copulatrix well developed. Lang's vesicle large.

Key to *Paraplanocera* species from African waters

1 With reddish submarginal band dorsally; spermiducal bulbs open into posterior chamber of prostate .... ***marginata***
1′ Without submarginal band; spermiducal bulbs open into prostatic duct .... ***aurora***

Paraplanocera aurora Laidlaw, 1903

LOCALITY. Coast of Zanzibar (Laidlaw, 1903). Known also from Sri Lanka (Laidlaw, 1904).

DESCRIPTION. Laidlaw, 1903*a*:102. Prudhoe, 1945:200.

Paraplanocera marginata Meyer, 1922

Paraplanocera rubrifasciata Kato, 1937

LOCALITIES. Red Sea (Meyer, 1922); on sand-flats of Bamburi, near Mombasa, Kenya (Prudhoe, 1945); Tor, Red Sea, 3.1.1957 (H. Steinitz *leg.*). Known also from Japan and the Persian Gulf.

DESCRIPTIONS. Meyer, 1922:139; Prudhoe, 1945:195.

NOTE. Dr Steinitz found the 'Body yellowish. Margin with a garland-like pattern of violet. Central portion of ventral side white'. The present writer has also seen a specimen from Australia with a white body bearing a narrow submarginal band of black.

Genus *DISPAROPLANA* Laidlaw, 1903

DIAGNOSTIC FEATURES. Body elongate, without tentacles. Eyes in two elongate clusters alongside cerebral organ. Mouth anterior to middle of body. Genital pores adjacent. Seminal vesicle bulbous; prostate not interpolated, opens directly into cirrus-sac alongside opening of ejaculatory duct; cirrus-sac relatively small, lined with spines. Thick musculature envelops prostate and cirrus-sac. Female antrum spacious; 'shell'-chamber short; Lang's vesicle small.

Disparoplana dubia Laidlaw, 1903

LOCALITY. East Africa (Zanzibar) (Laidlaw, 1903).

DESCRIPTION. Laidlaw, 1903*a*:103.

Family CALLIOPLANIDAE Hyman, 1953

DIAGNOSTIC FEATURES. Discoid or oval forms. Nuchal tentacles well developed, with eyes in lower half of each tentacle; cerebral eyes in two clusters between tentacles. Pharynx in mid-third of body. Genital pores adjacent to one another, well separated from posterior margin of body. Male copulatory complex anterior to its pore; with spermiducal bulbs or seminal vesicle; prostate vesicular, independent, dorsal to ejaculatory duct or seminal vesicle. Vagina long and narrow, thrown into an anteriorly-directed loop.

Key to callioplanid genera from African waters

1 Lang's vesicle horseshoe shaped .... ***Callioplana***
1′ Lang's vesicle bulbous .... ***Stylochoposthia***

Genus *CALLIOPLANA* Stimpson, 1857

DIAGNOSTIC FEATURES. Oval forms with prominent tentacles. Intestinal branches occasionally anastomosing. Seminal vesicle small, elongate, thin-walled; prostate small elongate, dorsal to seminal vesicle. Ejaculatory duct and prostatic duct pass through penis-papilla to open into male antrum. No penis-pocket. Vagina long, dorsal to male complex. Lang's vesicle horseshoe-shaped, with anteriorly-directed limbs.

Callioplana marginata Stimpson, 1857

LOCALITY. Inhaca I., Mozambique (on sand-flats in front of Marine Biol.Station (V. Gabie *leg.*) and under stones at low tide (M. Beverley-Burton *leg.*).) Known also from Sri Lanka, Japan and Australia.

DESCRIPTIONS. Yeri & Kaburaki, 1918:32; Stummer-Traunfels, 1933:3561; Kato 1944:289.

Genus *STYLOCHOPOSTHIA* Faubel, 1983

Faubel (1983) erected the genus *Stylochoposthia* for *Pseudostylochus bellus* Hyman, 1959, presumably because it possesses a common genital pore and a penial stylet, features not known to occur among other species assigned to the genus *Pseudostylochus*. The new species of *Stylochoposthia*, described below, is also without these two features, but in agreement with *S. bella* it has a very long looped vagina which extends anteriorly well beyond the male copulatory complex not found in *Pseudostylochus*. The new species requires *Stylochoposthia* to be redefined.

DIAGNOSTIC FEATURES. Broadly-oval or discoid forms of firm consistency. Tentacles well developed; ring of eyes at base of each. Cerebral eyes in two loose clusters between tentacles. Pharynx with 5 or 6 pairs of lateral folds. Male copulatory complex elongate, enclosed in thick sheath of connective tissue. Seminal vesicle muscular and fusiform; small prostate lined with tall epithelium thrown into longitudinal folds. Long vagina forming an anteriorly-directed loop dorsally to male complex. Lang's vesicle small and bulbous. Uterine canals not anteriorly confluent.

Stylochoposthia inhacae sp.nov.

LOCALITY. West shore coral reef between village and Marine Biol.Stat., Inhaca I., Mozambique (V. Gabie *leg.*) B.M.reg. no.1985.7.8.27–30 (syntypes).

DESCRIPTION (Fig.15). Body up to 63 mm in length and 50 mm in maximum width. Dorsal surface of the living worm is yellowish brown speckled with brown, except for a narrow marginal band clear of such markings. In the lateral fields of the dorsal surface, there is an irregular row of bluish areolae larger than the brown speckles. The pharynx and uterine canals appear as red-brown longitudinal bands, and the copulatory complexes as a somewhat trilobed reddish brown mass. Ventrally, the body is also yellowish brown, but with no speckling.

A pair of long reddish brown tentacles is situated at about one-third of the body-length from anterior margin. Arrangement of eyes typical of family Callioplanidae (Fig.15). Mouth in mid-third of body; pharynx with 5 pairs of lateral folds; intestinal branches appear not to anastomose.

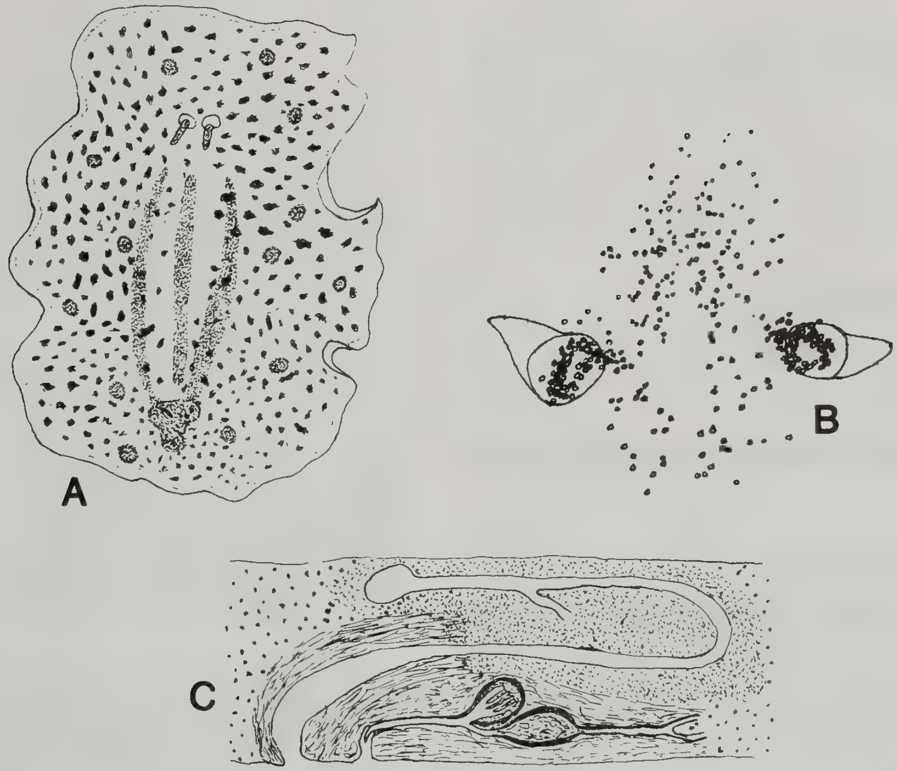

Fig.15 *Stylochoposthia inhacae*: A, dorsal surface of body in life; B, tentacles and eyes; C, sagittal section of copulatory organs.

Male genital pore at about 0.2 mm anteriorly to female, which lies at about 2 mm from posterior margin of body. Male copulatory complex lies anteriorly to its pore. Thin-walled sperm-ducts arise at a level a little posteriorly to that of the genital pores and extend anteriorly to beyond the male complex. At this point they become convoluted, much swollen and turn towards the median line, where they unite to form a narrow duct lying ventrally to the 'shell'-chamber of the female complex. This duct, a vas deferens, is relatively long and runs posteriorly to open into an elongate muscular seminal vesicle. Postero-laterally to the seminal vesicle, lies a small rounded prostate lined with a tall glandular epithelium thrown into four deep longitudinal folds arising from the anterior wall. From the seminal vesicle, an ejaculatory duct runs posteriorly and at a point ventrally and posteriorly to the prostate it receives a short prostatic duct to become a ductus communis. This duct is long and enclosed in a thick sheath of connective tissue and extends posteriorly to a small unarmed penis-papilla lying in the male antrum.

From the female genital pore, the vagina is thrown into a long anteriorly-directed loop reaching in the dorsal parenchyma to a level beyond the male copulatory organs. The vagina externa runs antero-dorsally to above the prostate where it becomes the vagina media. It is enclosed along its length by a thick sheath of connective tissue. The vagina media or 'shell'-chamber is invested with an exceptionally large mass of 'shell'-glands. At its anterior limit, the vagina turns sharply posteriorly near the dorsal wall of the body, soon to receive the common uterine duct and terminate in a very small Lang's vesicle. Uterine canals anteriorly separated.

Superfamily **CESTOPLANOIDEA** Poche, 1926, emend. Prudhoe (1982*a*)

DIAGNOSTIC FEATURE. Eyes widely distributed over cephalic region of body, except in marginal zone.

Key to cestoplanoid families from African waters

1 Pharynx in posterior third of body .... ***Cestoplanidae***
1′ Pharynx in anterior third of body . . ***Emprosthopharyngidae***

Family **CESTOPLANIDAE** Lang, 1884

DIAGNOSTIC FEATURES. Elongate to ribbon-like forms, sometimes with a ventral, adhesive pad near posterior end of body. Tentacles absent. Eyes numerous, distributed fanwise anteriorly from just posterior to cerebral organ to sub-marginal zones of cephalic region. Mouth and pharynx posterior; intestinal trunk long, with many pairs of non-anastomosing branches. Testes and ovaries in rows alongside intestinal trunk. Genital pores separate. Male copulatory complex dorsal or posterior to its pore; seminal vesicle well developed; prostate pyriform, interpolated and lined with smooth epithelium; penis-papilla variably developed. Duplicate male complex may occur. Vagina short, in dorso-posterior loop; 'shell'-chamber spacious, often dorso-ventrally compressed. Lang's vesicle may be present.

Genus ***CESTOPLANA*** Lang, 1884

DIAGNOSTIC FEATURES. With characters of family

Key to *Cestoplana* species from African waters

1 With multiple female copulatory complexes .... ***polypora***
1′ With single female copulatory complex 2

2 Dorsal surface of body with 3 longitudinal bands of red .... ***rubrocincta***
2′ Dorsal surface with 3 longitudinal bands of yellow .... ***filiformis***

Cestoplana rubrocincta (Grube, 1840)

Localities. Under stones at low tide, Boa Vista, Cape Verde Is (Laidlaw, 1906); East Beach, Pram Pram, Ghana (Miss M. A. Tazelaar *leg.*). Known also from English Channel, the Mediterranean and Japan.

Descriptions. Lang, 1884:516; Stummer-Traunfels, 1933: 3573; Kato, 1937*a*:225.

Cestoplana filiformis Laidlaw, 1903

Locality. East African coast (Laidlaw, 1903).

Description. Laidlaw, 1903*a*:110.

Note. Kato (1937*a*) regarded this species as a variety of *C. rubrocincta*.

Cestoplana polypora Meyer, 1922

Locality. Koseir, Red Sea. (Meyer, 1922).

Description. Meyer, 1922:149.

Note. Faubel (1983) erected the genus *Cestoplanoida* for this species on account of its multiple female copulatory complexes.

Family **EMPROSTHOPHARYNGIDAE** Bock, 1913

Diagnostic features. Elongate-oval forms, without tentacles. Cerebral and tentacular eye-clusters distinct, the latter slightly posterior to level of former; submarginal eyes arranged in an irregular band of varying width and length; few frontal eyes may lie between submarginal eyes and cerebral eye-clusters. Pharynx closely posterior to cerebral organ; intestinal trunk reaching to copulatory organs; intestinal branches not anastomosing. Genital pores separated in posterior region of body. Male copulatory complex anterior to its aperture. Vasa deferentia unite to form a long muscular canal leading to muscular seminal vesicle; pyriform prostate interpolated, with smooth epithelium, its distal end forms base of penis-papilla, occasionally bearing a stylet. Vagina forms a short anteriorly-directed loop; Lang's vesicle absent; uterine canals anteriorly separated.

Genus *EMPROSTHOPHARYNX* Bock, 1913

Diagnostic features. With characters of family.

Emprosthopharynx vanhoffeni Bock, 1931

Locality. Sao Vicenta, Porto Grande, Cape Verde Is and Morocco (Bock, 1931); Port Etienne, Mauretania (de Beauchamp, 1951*b*); near Accra, Ghana, 9.9.1955 (J. D. Thomas *leg*).

Description. (Fig.16). Bock, 1931:268.

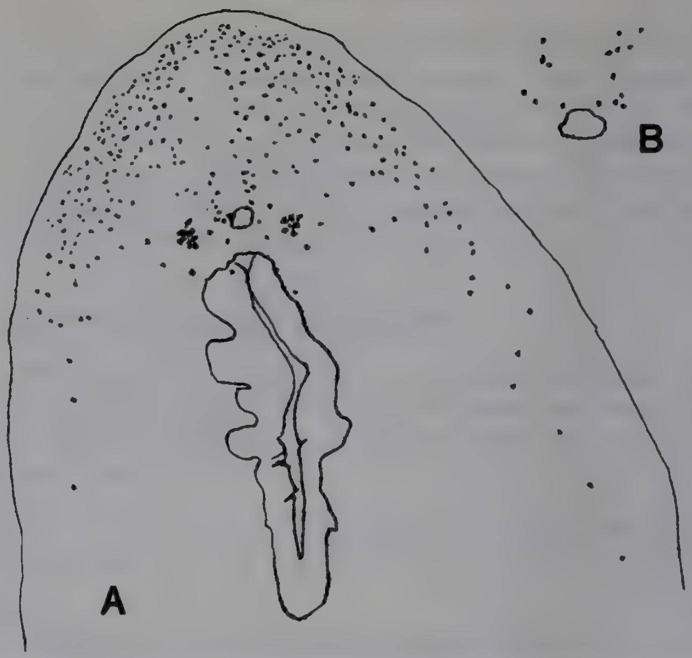

Fig.16 *Emprosthopharynx vanhoffeni*: A, dorsal view of anterior region of body; B, cerebral eyes (ventral view).

Note. The Ghanaian specimen is immature and much larger than the type-specimen of *E. vanhoffeni*, and the submarginal band of eyes extends much farther posteriorly.

Suborder **COTYLEA** Lang, 1884

Diagnostic features. Body with ventral sucker placed posteriorly to female genital pore—occasionally wanting. Tentacles when present antero-marginal, except in families Stylochoididae and Opisthogenidae in which nuchal tentacles occur. Eyes often in groups at base of tentacles and/or in marginal band on anterior margin of body; cerebral eyes in two short elongate groups, or in conical or rounded clusters over cerebral organ. Pharynx tubular, campanulate or ruffled. Prostate often independent. 'Shell'-gland normally swollen, but dorso-ventrally compressed. Uterine canals extend posteriorly from vagina (except in Boninidae and Pericelididae, in which the canals form an H-shaped figure). Lang's vesicle rarely present.

Key to cotylean families from African waters

1	Mouth and pharynx in anterior third of body	2
1′	Mouth and pharnyx in middle or posterior third of body	5
2	Pharynx tubular or campanulate	3
2′	Pharynx ruffled or irregularly ring-like	4
3	Without tentacles	***Prosthiostomidae***
3′	Tentacles marginal	***Euryleptidae***
4	Nuchal tentacles; male copulatory complex posterior to female	***Opisthogeniidae***
4′	Marginal tentacles; male complex anterior to female	***Pseudocerotidae***
5	Without tentacles	***Anonymidae***
5′	Tentacles marginal	6
6	Male complex with one or more prostatoids	***Boniniidae***
6′	Male complex without prostatoids	***Pericelididae***

Family **BONINIIDAE** Bock, 1913

Diagnostic features. Elongate body with two lateral lappet-like appendages on anterior margin. Adhesive organ as a rounded depression in posterior region of ventral surface of body. Eyes anterior, chiefly marginal or submarginal, with remaining few eyes in cerebral region. Long ruffled pharynx in mid-third of body; intestinal trunk long; intestinal branches not anastomosing. Genital pores separated. Testes and ovaries in dorsal parenchyma. Male copulatory complex posterior to pharynx, with unarmed penis-papilla and includes single prostatoid with stylet or several such organs opening into male antrum or on ventral surface of body. Vagina with dilated, dorso-ventrally compressed 'shell'-chamber. Lang's vesicle developed. Uterine canals form H-shaped figure bearing vesicles.

Genus ***TRAUNFELSIA*** Laidlaw, 1906

Diagnostic features. Vasa deferentia open directly into base of small penis-papilla; no seminal vesicle or prostate. Single prostatoid posterior to conical penis-papilla and opening into depression on ventral surface of body. On each side of penis-papilla, narrow canal opens into male antrum and terminates inwardly by branching into number of small chambers invested with large gland cells.

Traunfelsia elongata **Laidlaw, 1906**

LOCALITY. From among weeds on sandy shore, Cape Verde Is (Laidlaw, 1906).

DESCRIPTION. Laidlaw, 1906:714.

Family **ANONYMIDAE** Lang, 1884

DIAGNOSTIC FEATURES. Broadly-oval forms with ventral sucker, but without tentacles. Eyes along margin of body and in two groups over cerebral organ. Mouth more or less centrally situated; pharynx with four pairs of deep lateral folds. Male complex with many pyriform organs arranged in a longitudinal row in each lateral field of body. Each organ is composed of seminal vesicle and conical unarmed penis-papilla lying in penis-pocket; without prostate. Female copulatory complex simple, anterior to ventral sucker and closely posterior to mouth.

Genus *ANONYMUS* Lang, 1884

DIAGNOSTIC FEATURES. With characters of family.

Anonymus virilis **Lang, 1884**

LOCALITY. Among nullipores in 5–9 metres, St Vincent Harbour, Cape Verde Is (Laidlaw, 1906).

DESCRIPTIONS. Lang, 1884: 522; Stummer-Traunfels, 1933:3576.

Family **PERICELIDIDAE** Laidlaw, 1902, emend. Poche, 1926

DIAGNOSTIC FEATURES. Broadly-oval forms with two small widely-separated, anterior, marginal tentacles, each bearing eyes. Ventral sucker posterior. Marginal eyes round body; cerebral eyes in two elongate clusters; frontal eyes present. Pharynx ruffled, in mid-third of body. Genital pores united or closely approximate, between pharynx and ventral sucker. Male copulatory complex anterior to male pore. Seminal vesicle distinct; no distinct prostate, but proximal region of ejaculatory duct is lined with eosinophilic gland-cells when male phase is active. Penis-papilla small, without stylet or penis-sheath. Vagina simple; 'shell'-chamber dilated and dorso-ventrally compressed. Uterine canals extend anteriorly from proximal end of vagina, with several uterine vesicles, occasionally uteri form H-shaped figure.

Genus **PERICELIS** Laidlaw, 1902

DIAGNOSTIC FEATURES. With characters of family.

Pericelis byerleyana **(Collingwood, 1876) Laidlaw, 1906**

Typhlolepta byerleyana Collingwood, 1876

LOCALITIES. Eylath, Gulf of Aqaba, Red Sea, May–Dec. 1951–1955 (H. Steinitz *leg.*); on a *Porites* in high reef of Iles Muscha, Gulf of Tadjourrah, Djibouti (Meixner, 1907). Widely distributed in the Indo-W. Pacific region in the area bounded by East Africa, Indonesia, Fiji and the Great Barrier Reef.

DESCRIPTIONS. Collingwood, 1876:92; Laidlaw, 1902:291; Meixner, 1907:473.

Family **OPISTHOGENIIDAE** Palombi, 1928

DIAGNOSTIC FEATURES. Oval forms with nuchal tentacles containing eyes. Ventral sucker central. Marginal eyes anterior; cerebral eyes in oblong group between tentacles. Mouth anterior; pharynx ruffled in anterior third of body; intestinal trunk long; intestinal branches anastomosing. Male genital pore ringed by large gland-cells, between ventral sucker and posterior margin of body. Vasa deferentia extend from pharyngeal region to posteriorly-placed male copulatory complex. Seminal vesicle anterior to male pore; independent prostate posterior to pore; penis-papilla small, without stylet. Female genital pore between pharynx and ventral sucker. Female complex anterior to its external opening. Vagina simple; uterus consists of two lateral groups of narrow reticulate canals opening into proximal end of vagina.

Genus **OPISTHOGENIA** Palombi, 1928

DIAGNOSTIC FEATURES. With characters of family.

Opisthogenia tentaculata **Palombi, 1928**

LOCALITY. Dredged at Kubri, Suez Canal (Palombi).

DESCRIPTION. Palombi, 1928:608.

Family **PSEUDOCEROTIDAE** Lang, 1884, emend. Poche, 1926

DIAGNOSTIC FEATURES. Broadly-oval or elongate body varying considerably in size; dorsal surface may be papillate. Ventral sucker more or less central. Two tentacular lobes formed by folds on the anterior margin of the body. Each tentacle usually with eyes; cerebral eyes in a rounded, conical or transversely arcuate cluster or in two elongate groups over the cerebral organ. Ruffled pharynx immediately posterior to cerebral organ; intestinal trunk extends from pharynx to posterior region of body and bears several pairs of anastomosing lateral branches. Genital pores between pharynx and ventral sucker. One or two sets of male copulatory organs closely posterior, or partly ventral, to pharynx. Vasa deferentia extending anteriorly from the posterior region of the body to enter a seminal vesicle. Prostate relatively small, independent; penis-papilla small, generally with short stylet and enclosed in penis-pocket. Female copulatory complex almost invariably single, lying closely posterior to male. Vagina short, arcuate; 'shell'-chamber dilated and dorso-ventrally compressed. Uterine canals form H-shaped figure connected with an anastomosing system of oviducts; uterine vesicles may be present.

Key to pseudocerotid genera from African waters

1 Without tentacular eyes .... ***Parapseudoceros***
1′ With tentacular eyes 2

2 Dorsal surface of body smooth .... ***Pseudoceros***
2′ Dorsal surface of body papillate .... ***Thysanozoon***

Genus ***PSEUDOCEROS*** Lang, 1884

DIAGNOSTIC FEATURES. Dorsal surface smooth, often brilliantly coloured. With tentacular eyes. Pharynx with four or five pairs of lateral folds. Male copulatory complex single or duplicated; in latter instance they are symmetrically arranged on either side of median line.

NOTE. There exists confusion concerning specificity in the genus *Pseudoceros*, for its species show a very high degree of uniformity in their general structure. Hyman (1954*a*) discussed the constitution of the genus and points to the problem of separating species on morphological grounds and suggests that coloration and markings of the body may be accepted as the means of distinguishing one species from another. Nevertheless, the present writer has found that colour in a species may be variable, but the arrangement of markings is reasonably constant. For instance, *Pseudoceros bedfordi*, *P. velutinus* and *P. zebra* may be readily recognized by their markings alone, irrespective of their colour. Unfortunately, preserved specimens often lose their coloration and markings completely, thus such specimens without notes on coloration and markings or some other form of representation, especially a painting or a colour-photograph, during life are very difficult, if not impossible, to determine specifically with any degree of certainty. It seems, therefore, that a close examination of superficial features is needed to assess their diagnostic value, and this should be done on living specimens.

Later, Hyman (1959) said 'Whether the male apparatus is single or paired is a useful character and details of the male copulatory apparatus may be of value in specific diagnosis' and went on to say that 'It now appears that the shape of the pharynx may be decisive. In most species, the pharynx has a compact outline but several species are now known in which the pharynx takes what I have termed the butterfly shape, putting out lateral lobulations that increase in length in the antero-posterior direction. ... ' The shape of the pharynx in pseudocerotids as a diagnostic feature is debatable, because in a young worm the pharynx has a 'compact outline', but as the worm grows so the pharynx finally assumes a 'butterfly shape'. Moreover, fixatives tend to cause the pharynx to contract, sometimes appearing as a mere rosette.

The number of male copulatory complexes is also questionable as a diagnostic feature, particularly at generic level, as proposed by Faubel (1984). Lang (1884) appears to have no doubts, because he described three varieties of *Pseudoceros maximus*, one with a single male complex and a single opening, one with two complexes, each with its own opening, and one with two complexes, but with only one opening. Stummer-Traunfels (1895) commenting on Lang's three varieties considered that each is worthy of specific recognition, but refrains from giving them names. Later, the same author (1933) figured two original specimens of *Pseudoceros latissimus* (Schmarda, 1859), one with a single male complex and the other two complexes, and clearly considers them to belong to the same species, thus implicitly discarding his earlier notion on speciation. Faubel (1954), however, renamed the specimen of *P. latissimus* with two complexes as *Pseudobiceros schmardae* sp.nov. In fact, Faubel employed a single or double male complex and the presence or absence of a penis-stylet as means of dividing the genus *Pseudoceros sensu* Lang into five genera, four of which are defined as new, but are, in the present writer's opinion, of doubtful validity. Marcus & Marcus (1951:15) stated that the penis-stylet in polyclads appears late in the development of the male complex in polyclads, as the present writer has found in the present investigation. In pseudocerotids, the stylet is merely a cuticle investing a slender conical penis-papilla, and in *Pseudoceros bifasciatus* n. sp. (see below) a not fully mature specimen shows no penis-stylet, whereas a fully mature one does. There is also the possibility of the cuticle covering the papilla being shed at the end of the male phase, as happens in some proseriate turbellarians. It therefore seems likely that the male complex in any species of *Pseudoceros* bears a penis-stylet at some stage in its development.

The occurrence of supernumerary organs is well known among certain families of polyclads, and there are instances of two ventral suckers, multiple female organs and double male copulatory complexes among species of *Pseudoceros sensu* Lang. The rigid acceptance of these features as systematically important is doubtful, because so little is known of morphological variation among polyclads. Looking among triclad turbellarians, instances of the development of supernumerary reproductive organs are known among individual species of the genus *Dugesia*, and there seems to be no reason why such should not occur among individual species of polyclad genera, e.g., the genus *Cestoplana*.

The writer, therefore, refrains from accepting Faubel's classification of the family Pseudocerotidae and recognizes the generally accepted scheme outlined by Bresslau (1933).

***Pseudoceros albicuneatus* sp.nov.**

LOCALITY. Opposite Marine Biol. Stat., Inhaca I., Mozambique, 11.7.1961 (V. Gabie *leg.*).

DESCRIPTION (Fig.17). Body broadly oval, 6 mm in length after fixation in Susa. Dorsal surface yellowish, dotted with light brown and bearing 12 large white spots, 6 in each lateral field of body. Median line covered with a broad band of white. Broad marginal band of black, irregularly interrupted with cuneiform patches of white. Tentacles bearing black marginal band.

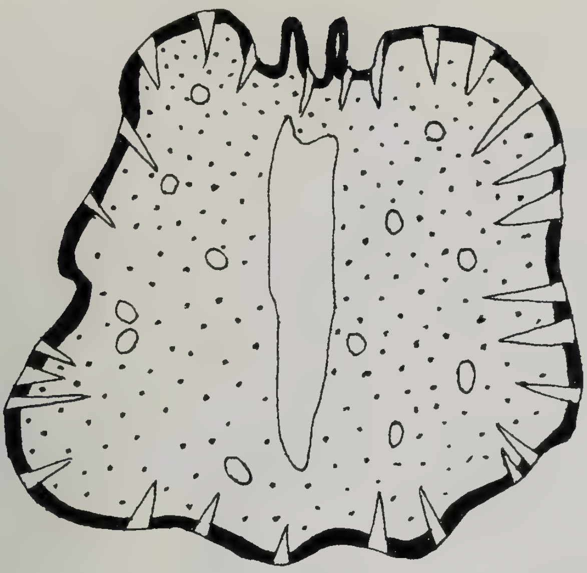

Fig.17 *Pseudoceros albicuneatus*, dorsal surface of body in life.

Note. No specimen available for study. Known only from a water-colour painting of the living worm. B.M.reg.no. 1985.7.5.2. The coloration and markings of the dorsal surface of the body are definite and enable the species to be readily recognized.

Pseudoceros albimaculatus sp.nov.

Locality. Low tide, west coast of Inhaca I., Mozambique, July, 1958 (V. Gabie *leg.*) B.M.reg.no. 1985.7.5.3–6.

Description (Fig.18). Oval forms narrowing somewhat anteriorly and rounded posteriorly; 13–24 mm in length and 8–10 mm in maximum width. Disposition of eyes as shown in Fig.18. In a water-colour painting of the living worm, the dorsal surface is reddish violet, with transverse marginal patches finely stipled with white and along median line there are elongate patches likewise stipled with white. Marginal tentacles are prominent in the living worm, but retracted beyond recognition in preserved specimens, as shown in Fig. 18. One male pore; penis-papilla with stylet. The male copulatory complex shows no specific differences from that of other species of *Pseudoceros*, where the complex has been described.

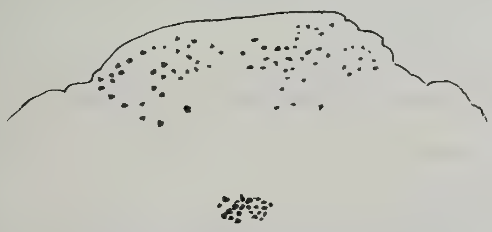

Fig.18 *Pseudoceros albimaculatus*, marginal and cerebral eye-clusters (dorsal view).

Pseudoceros albireticulatus sp.nov.

Locality. On south barrier reef, 13°04′S. 45°0.9′E., Benthedi, Mayotte, Comoro Is, 27.3.1977 (P. Bouchet *leg.*) B.M.reg. no. 1984.10.16.6.

Description. The only specimen available is immature and fragmentary, but the preserved fragments suggest that the worm measured about 5 mm in length. Ventral sucker lies a little anteriorly to middle of body. The marginal tentacles are mere humps, each containing about 16 eyes, with a few eyes between the tentacles. The fragment containing cerebral eyes is missing, but a colour-transparency of the living worm suggests that there is a cluster of about 12 cerebral eyes. The transparency also shows that the dorsal surface of the body is reddish, with a dense network of thin rosy-white lines. The marginal regions anteriorly are distinctly lighter in colour than the remainder of the body.

Note. The coloration and markings are the specific features of this new form.

Pseudoceros bedfordi Laidlaw, 1903

Pseudobiceros bedfordi (Laidlaw) Faubel, 1984

Locality. In front of Marine Biol. Stat., Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*); known also from Singapore (Laidlaw, 1903), Indonesia (Bock, 1913), Palau Is (Kato, 1943), Vietnam (Dawydoff, 1952), Great Barrier Reef (Hyman, 1954*a*), Caroline Is (Hyman, 1959*b*).

Description. Represented by a water-colour painting by Dr Gabie and identified by Dr Libbie Hyman. The painting suggests that, when alive, the worm was elongate and measured 100 mm in length, but after preservation Dr Gabie found it to measure 35 mm by 36 mm. The coloration of this species is beautiful and variable. The ground-colour of the dorsal surface varies from dark green, dark brown to purplish brown covered with transverse arcs, stripes and spots of yellowish white, pink or buff, extending laterally from the median line. Margin of body of a darker hue and may be spotted with green. Ventral surface of body lighter in colour, without any pattern. Ventral sucker central. Marginal tentacles distinct. From ventral side of body numerous eyes are clearly seen on the margins of the tentacles. Cerebral eyes numerous, gathered into an oval cluster. Two male complexes. Descriptions have been given by Laidlaw (1903*b*:314), Bock, (1913:254) and Kato (1943:87).

Note. *P. bedfordi* was briefly described by Laidlaw from a damaged specimen found in Singapore Harbour. Bock (1913) described and figured the external features of a specimen from a coral reef on Mendanao, west of Pulau Belitung (Billiton) I. Mendanao is an Indonesian island lying between Borneo and Sumatera (Sumatra). Kato (1943) in recording the species from the Palau Is appears to have thought that Mendanao was Mindanao in the Philippines and Hyman (1954*a*) added confusion by stating that Bock recorded his specimen from 'off Billiton on the island of Mindanao in the Philippines'.

Pseudoceros bifasciatus sp.nov.

Locality. At low tide, west coast of Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*) B.M.reg.nos. 1985.7.5.8 (holotype), 1985.7.5.9–13 (paratypes).

Description (Fig.19). The body measures up to 53 mm in length and 30 mm in maximum width after fixation in FAA. The preserved specimens are deep brown dorsally, with a distinctly lighter marginal band, and brownish ventrally. In a water-colour painting of the living worm, the body is elongate, somewhat rounded anteriorly and narrowing posteriorly. This painting shows that the dorsal surface of the

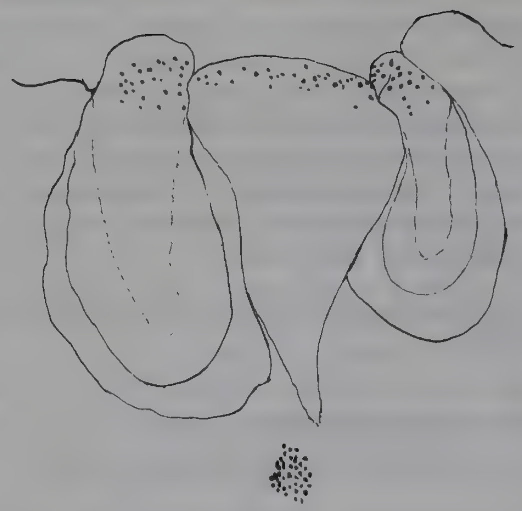

Fig.19 *Pseudoceros bifasciatus*, cephalic region of body (dorsal view).

body is bordered with two narrow bands, the outer being orange coloured, the inner white. The ground-colour in the median region of the body is deep purple, gradually fading to pale bluish green on reaching the white submarginal band. On each side of the median line, there is a broad lanceolate band of black. The ventral surface of the body is purplish. Marginal tentacles represented by a pair of folds of the anterior margin of the body; they bear the orange and white marginal bands. Ventral sucker situated more or less centrally. Eyes occur in the anterior region of each tentacle and in the margin of the body between the tentacles. Cerebral eyes disposed dorsally to cerebral organ and appear as a single cluster or in three ill-defined arcuate rows. Mouth in anterior fifth of body and opens into middle of short pharyngeal chamber enclosing a large pharynx with four pairs of deep lateral folds. Slender intestinal trunk extends to near hind end of body and gives off many pairs of lateral limbs, the branches of which anastomose profusely.

Ventral testes and dorsal ovaries are widely distributed, but do not occur in the cerebral, tentacular and peripheral regions of the body. The copulatory organs were removed from a preserved specimen measuring 30 mm long and 20 mm wide and longitudinally sectioned. Unfortunately, the resulting sections show the worm not to be fully developed. The single male complex is only partially developed, showing an elongate seminal vesicle lying posteriorly to the male pore, and a penis-papilla without a distinct stylet and enclosed in a penis-sheath. The prostate is little developed and gives no indication of its ultimate size in relation to that of the seminal vesicle. Closely posterior to the male complex in this specimen lies a mass of gland-cells probably representing *Anlagen* of the female complex. The largest specimen has not been sectioned, but examined as a whole mount cleared in methyl saicylate. It has well-developed copulatory organs situated in anterior fifth of body, with an elongate seminal vesicle which is about three times larger than the globular prostate lying dorsally to the male pore. Its penis-papilla has a stylet. The female copulatory complex is typical of the genus *Pseudoceros*, with a wide 'shell'-chamber dorso-ventrally compressed and with uterine canals extending posteriorly to about middle level of body. It is worthy of note that the penis-papilla in the immature specimen is without a stylet which is present in the mature worm.

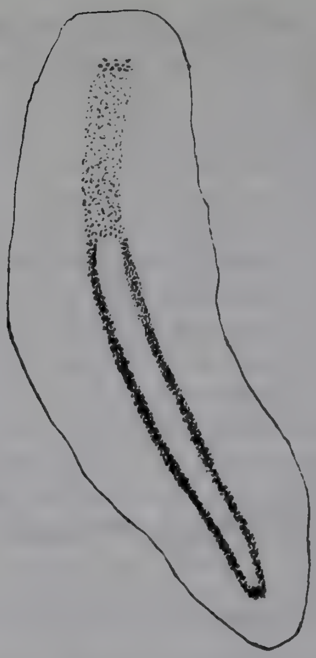

Fig.20 *Pseudoceros bifurcus*, dorsal surface of body in life.

Pseudoceros bifurcus sp.nov.

LOCALITY. In 38 metres, M'Sanga Tsohole Reef (12°42′S, 40°59′E), Benthedi, Mayotte, Comoro Is, 29.3.77 (P. Bouchet *leg*.). B.M.reg.no. 1984.10.6.7–8.

DESCRIPTION (Fig.20). The preserved specimens are brownish, but in a colour-transparency the living worm appears, when viewed dorsally, to be pale green, lightly tinged with mauve anteriorly and with a white marginal band. Along the median line, there is an orange-coloured band extending from the posterior border of the cerebral eye-cluster to about the junction of the anterior and middle thirds of the body, where the band bifurcates into narrow black or purplish bands running parallel with the median line and uniting posteriorly. Between the narrow bands the body is white. The body is elongate oval, 8–12 mm long and 5–6 mm wide. The anterior margin of the living worm is truncate, showing no indication of tentacles, whereas in one of the preserved specimens a pair of small tentacular folds of the anterior margin of the body occurs in the median region. The tentacles contain few eyes, and there are four or five marginal ones lying between the tentacles. Cerebral eyes arranged in an irregular cluster. Both specimens are immature.

Pseudoceros bimarginatus Meixner, 1907

LOCALITY. Among algae in Gulf of Tadjourrah, Djibouti (Meixner,1907,465).

DESCRIPTION (from Meixner). Preserved specimens 16–23 mm long and 11–13 mm wide. Ground-colour of living worm roseate dorsally and similarly coloured, but somewhat deeper, ventrally. Body-margin with inner band of golden yellow and outer band of chestnut-brown with green edging. Adult worms with mottling of reddish brown, with deeply ruffled pharynx showing whitish and uterine canals dark violet-grey. About 70 cerebral eyes in a rounded cluster. On dorsal surface and ventral margins of tentacles, eyes in one or two irregular rows, extending unbroken between tentacles. Pharynx with 5 or 6 pairs of deep lateral folds. Ovaries lateral to pharynx and widespread posteriorly to it; testes extend more anteriorly. Single male copulatory complex. Each

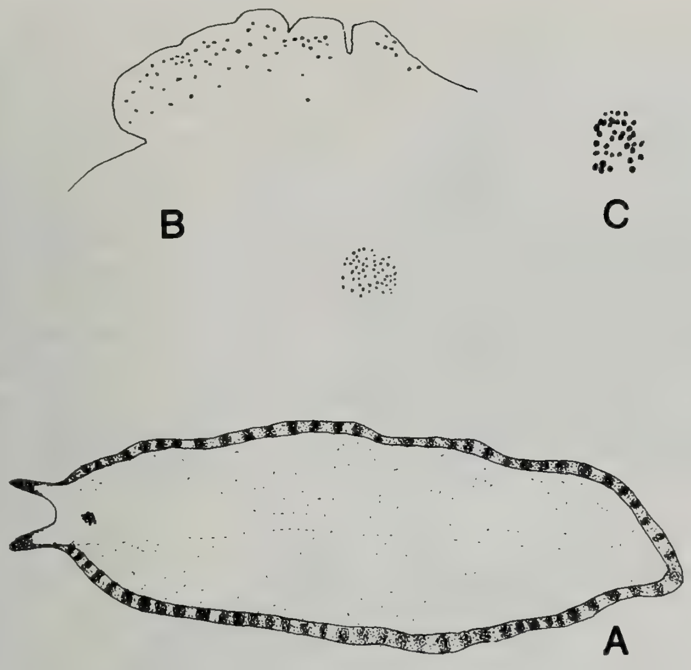

Fig.21 *Pseudoceros concinnus*: A, dorsal surface of body in life; B, cephalic region of body; C, tentacular eye-cluster.

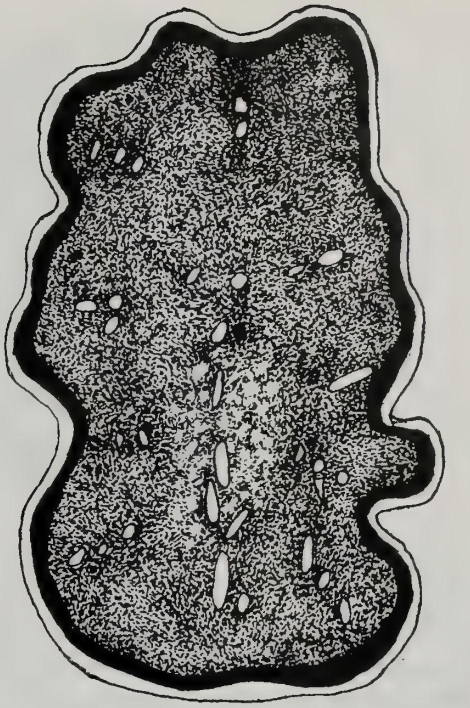

Fig.22 *Pseudoceros decorus*, dorsal surface of body in life.

uterine canal divides into three longitudinal branches lying dorsally to the vasa deferentia.

Pseudoceros caerleopunctatus Palombi, 1928

Locality. Kabret, Suez Canal, 18.11.1924. (Palombi, 1928).

Description (from Palombi). Elongate-oval forms, 14.5 mm long and up to 8 mm wide. Ground colour of dorsal surface creamy yellow; margins spotted with deep blue, each spot surrounded be a bluish areola of reticulate appearance. Outer branches of areolae do not anastomose so that the yellowish ground-colour extends between the blue spots. Blackish punctuation follows margin of body irregularly. Eyes unevenly distributed along anterior margin of body. Cerebral eyes numerous, arranged in two, symmetrically-disposed, pyriform clusters. Single male pore. Vasa deferentia proceed anteriorly, give off a pair of large swellings and continue inwardly to separately enter sides of well-developed pyriform seminal vesicle; prostate relatively small; penis-stylet present; male antrum narrow.

Pseudoceros concinnus (Collingwood, 1876) Kaburaki, 1923

Proceros concinnus Collingwood, 1876

Localities. In 3–30 metres, Mayotte, Comoro Is (P. Bouchet *leg.*); under rocks at South Point, Inhaca I., Mozambique (V. Gabie *leg.*).

Description (Fig.21). When alive, the body of specimens from Inhaca I. in the southern region of the Mozambique Channel, was elongate and measured 15–40 mm in length. Prominent marginal tentacles deep blue. According to a water-colour painting of the living worm, the ground-colour of the dorsal surface is pale lemon, with a greyish border. This border bears blue spots at regular intervals throughout its course. Dorsally, there is a median band, lighter than the ground-colour, wider anteriorly than posteriorly. All traces of coloration and markings have been lost in preserved specimens, which have become dark brown in alcohol or yellowish after fixation in Bouin's solution.

Ventral sucker weakly developed and situated in middle of body. Marginal tentacles with relatively few eyes; small accumulation of eyes over the cerebral organ. Pharynx with four pairs of deep lateral folds, the hinder pair of which are long alate projections extending posteriorly to about level of female genital pore. There appears to be one male copulatory complex. The copulatory organs of this species have been described by Hyman (1954*a*).

Immature specimens from the Comoro Is in the northern region of the Mozambique Channel have been assigned to this species, although their coloration and markings are, according to a colour-transparency, rather different from the Inhaca specimens. The ground-colour of the body is whitish, slightly tinged with yellow, the dorsal surface bears a median band of orange, and the margin of the body carries a series of large blue or mauve spots.

This species has also been recorded from Sabah, Malaysia (Collingwood, 1876), the Philippines (Kaburaki, 1923), Indonesia (Stummer-Traunfels, 1933), Irian Jaya (Dutch New Guinea) (Hyman, 1954*a*). These localities have provided specimens with variations in colour and markings. The identity of the specimens mentioned by Kaburaki and by Stummer-Traunfels are doubtful, and Hyman (1959) considers Stummer-Traunfels' specimens to be comparable to her new species *Pseudoceros tristriatus*.

Pseudoceros decorus sp.nov.

Locality. Lighthouse, Inhaca I., Mozambique, 12 July 1962 (V. Gabie *leg.*) B.M.reg.no. 1985.7.5.16 (Painting).

Description (Fig.22). No specimen available for study. The living worm in a water-colour painting is oval in outline and measures about 20 mm in length. Its dorsal surface is purplish with a pattern of white spots of various sizes, as shown in Fig.22. There are two submarginal bands, an outer one of yellow enclosing a broader one of deep purple. No tentacles are indicated in the painting.

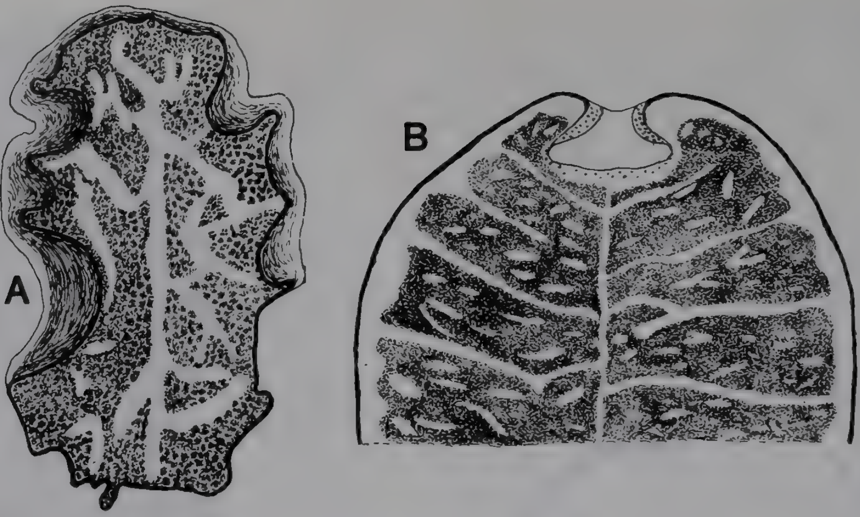

Fig.23 *Pseudoceros dendriticus*: A, dorsal surface of body in life; B, cleared preserved specimen.

NOTE. This form closely resembles *Pseudoceros kentii* Graff, in Saville-Kent, 1893, from the Great Barrier Reef, which is figured as being reddish brown dorsally with an outer band of yellow bordering a slightly wider band of reddish brown enclosing a narrow band of black or purple. If the two inner coloured bands were to mix it would then leave a broad band of deep purple similar to that of the Inhaca specimen. *P. kenti* is, however, without any white spots on the dorsal surface, but this feature might be incidental in the new species.

Pseudoceros dendriticus sp.nov.

LOCALITY. Inhaca I., Mozambique, July 1960 and 1962 (V. Gabie *leg.*) B.M.reg.no.1985.7.5.17–19.

DESCRIPTION (Fig.23). The following account is based on a water-colour painting of a living worm and three alcohol preserved specimens, which have lost coloration. A single specimen fixed in Susa measures about 45 mm long and up to 20 mm wide after being considerably flattened. The live specimen appears to have measured about 32 mm long and 20 mm wide. The dorsal surface of this specimen (Fig.23A) has a ground-colour of yellow profusely dappled with deep brown, leaving a median band of deep yellow, from which similarly-coloured branches extend to the margin of the body. This margin bears a narrow band of black, between which and the brown dapple, the body appears to be reddish brown. The ventral surface of the body is yellowish brown, but towards the margins the body becomes reddish brown with thin longitudinal flashes of black.

The three preserved specimens have lost all colour and design on the dorsal surface, but when cleared in methyl salicylate, they have a pale ground-colour bearing a pattern of brown, as shown in Fig.23B. A pale median line extends through the body and gives off at intervals similar lateral lines extending to the margins of the body, thus superficially giving the dorsal surface the appearance of bearing two longitudinal rows of brownish plates. There is also a narrow marginal band of black, separated from the brownish plates by the paler ground-colour. Ventrally, the body is light brown with a narrow black marginal band.

Marginal tentacles are not apparent in the painted worm, but in each of the preserved worms they appear as a pair of small folds of the anterior margin of the body. The tentacles each contain relatively few eyes and fewer in the bridge between the tentacles. The cerebral eyes are arranged in a conical cluster. Ventral sucker in mid-region of the anterior half of the body. Mouth opens into middle of pharyngeal chamber containing an elongate pharynx bearing 5 pairs of shallow lateral folds; intestinal trunk gives rise to a close network of canals. Reproductive system not yet developed in preserved specimens, but a pair of adjacent male genital pores occur near hind region of pharynx. Female genital pore not apparent.

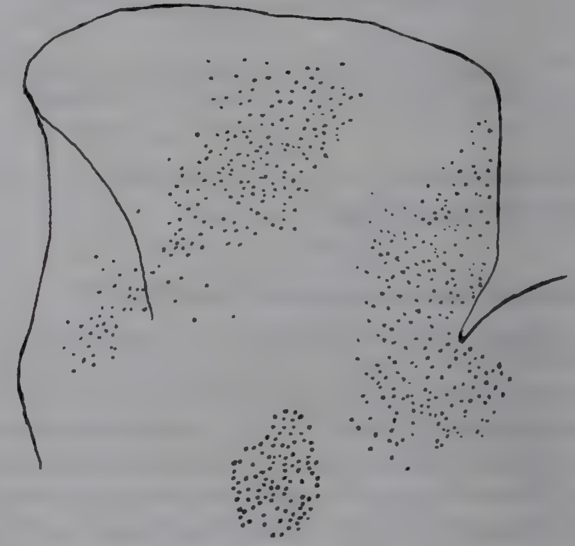

Fig.24 *Pseudoceros devisii*, arrangement of cerebral and tentacular eyes.

NOTE. The difference in the design on the dorsal surface of the living worm and that seen in the preserved worms is such as to suggest that the two represent different species, but the present writer is left with no reason to disagree with the collector's interpretation until shown to be otherwise.

Pseudoceros devisii Woodworth, 1898

LOCALITY. In front of Marine Biol. Station, Inhaca I. Mozambique, July 1958 (V. Gabie *leg.*) Hitherto known from the Great Barrier Reef (Woodworth).

DESCRIPTION (Fig.24). According to Woodworth's (1898:63) description the body is 'bright orange-yellow, with a broad marginal band of deeper orange and a prominent median dorsal ridge along which the pigment is denser than over the general surface of the body, though not so deep in colour as the marginal band. Length, 33 mm; greatest breadth, 16 mm.'

The specimen examined by the present writer was, when alive, elongate and measured about 15 mm long and up to 6 mm wide. Its dorsal surface is, as shown in a water-colour painting, yellowish with a tinge of green and bordered by a thin band of orange. The median area is somewhat brownish, with patches of white anteriorly and posteriorly and a small dark spot anteriorly indicating the presence of a diamond-shaped cluster of cerebral eyes.

When preserved, the specimen was much flattened and now measures about 22 mm long and 10 mm in maximum width. It is now greyish, showing no trace of the original colour or markings. The ventral sucker is centrally placed. Marginal tentacles not distinct, but each bears two or three hundred eyes.

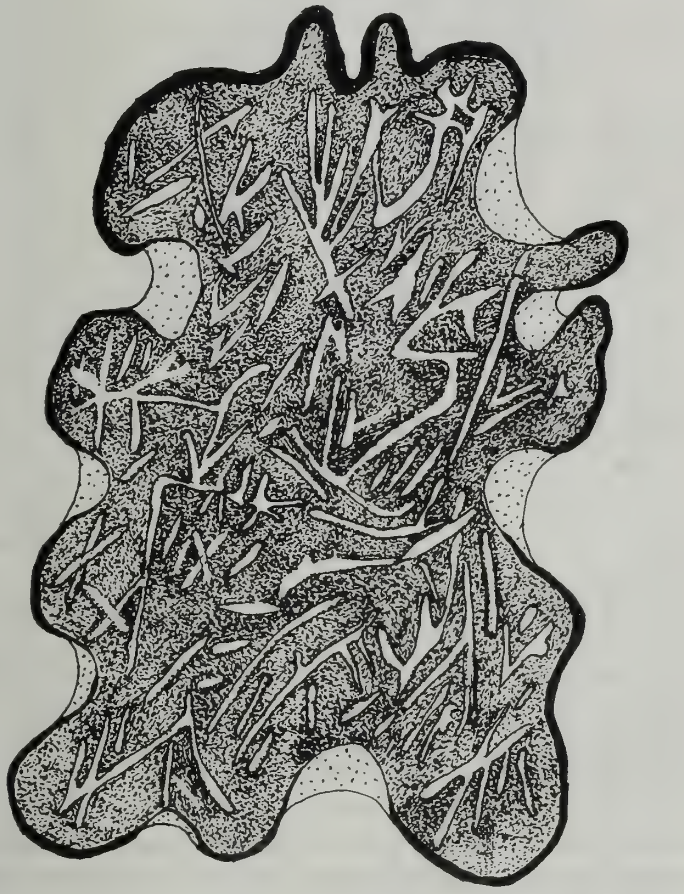

Fig.25 *Pseudoceros dubius*, dorsal surface of body in life.

Pseudoceros dubius sp.nov.

LOCALITY. Ponte Torres, Inhaca I., Mozambique, 11.7.1961 (V. Gabie *leg.*). B.M.reg.no. 1985.7.5.21 (Painting).

DESCRIPTION (Fig.25). No specimen available, but according to a water-colour painting of the living worm, the body is broadly oval with a deeply-folded margin. The dorsal surface is reddish brown and bears numerous scattered streaks or lines of yellow, sometimes merging with one another. There is a narrow marginal band of black. Ventral surface of body pinkish. Anterior marginal tentacles strongly developed and bearing the black marginal band.

Pseudoceros duplicinctus sp.nov.

LOCALITY. Opposite Marine Biol.Stat., Inhaca I., Mozambique, July 1960 (V. Gabie *leg.*). B.M.reg.no. 1985.7.5.22.

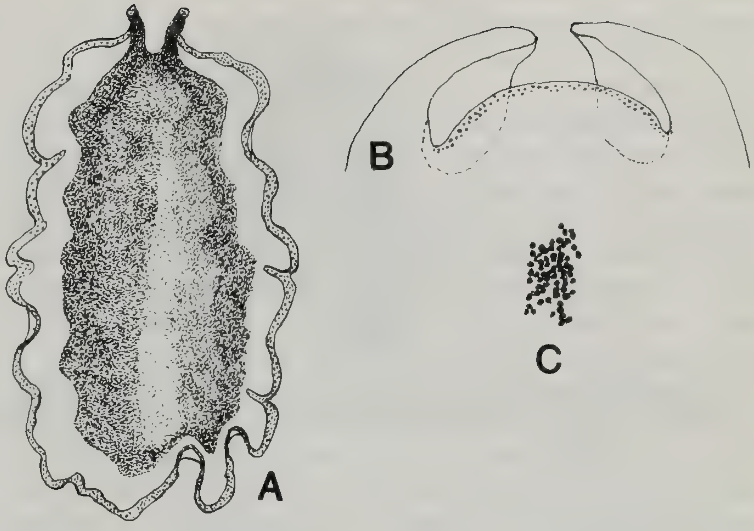

Fig.26 *Pseudoceros duplicinctus*: A, dorsal surface of body in life; B, cephalic region of body; C, cerebral eye-cluster.

DESCRIPTION (Fig.26). One preserved specimen available, and a water-colour painting of it when alive. Preserved in alcohol, the body is 48 mm in length and 32 mm in maximum width, and of ash-grey colour, being lighter in the marginal regions. The painting shows the dorsal surface of the body to be dark brown, lighter along the median line, more especially posteriorly. There is also a narrow marginal band of orange, bordering a wide band of pale blue. In the preserved condition, the tentacles appear as folds of the anterior margin of the body, but in the living worm they are prominent and brownish, tipped with orange. Shallow ventral sucker situated at about the junction of the anterior and middle thirds of the body. Eyes have not been detected in the tentacular folds, but appear to be confined to the margin of the body between the folds. Cerebral eyes in broad elongate mass over cerebral organ. Mouth in median line at about 10 mm posterior to anterior margin of body. It opens into middle of pharyngeal chamber containing a pharynx thrown into six pairs of deep lateral folds. Intestinal trunk narrow, extends from pharynx to posterior region of body, giving off along its course several pairs of lateral limbs, branches of which anastomose.

A single male copulatory complex lies closely posterior to pharynx, and, according to serial sections, is typical of other species of *Pseudoceros* in structure. Penis-papilla with stylet. Female complex likewise typical of the genus and bears no features which might be regarded as characteristic of the species.

NOTE. This species may be recognized by its colour and markings of the dorsal surface of the body and the apparent lack of eyes in the marginal tentacular folds. Heath and McGregor (1913) erected the genus *Licheniplana* for a new species, *L. lepida*, which has papillae on the dorsal surface of the body and no eyes in the marginal tentacles, but marginal eyes between the tentacles. In the present instance, the absence of eyes in the tentacular folds of the preserved specimen might be due to the considerable contraction of the tentacles at fixation, for the painting of this specimen when alive shows a pair of well-developed marginal tentacles.

Pseudoceros flavolineatus sp.nov.

LOCALITY. Northern Bay, Inhaca I., Mozambique, July 1960 and 1962 (V. Gabie *leg.*). B.M.reg.nos. 1985.7.5.25 (holotype), 1985.7.5.23–24 (paratypes).

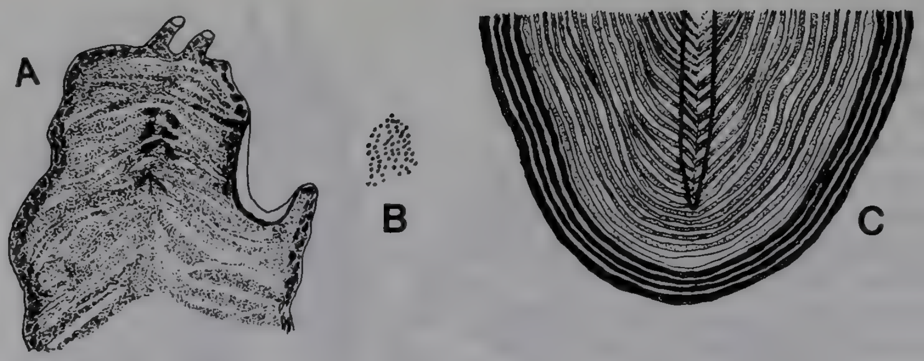

Fig.27 *Pseudoceros flavolineatus*: A, dorsal surface of body in life; B, cerebral eye-cluster; C, posterior region of cleared preserved worm.

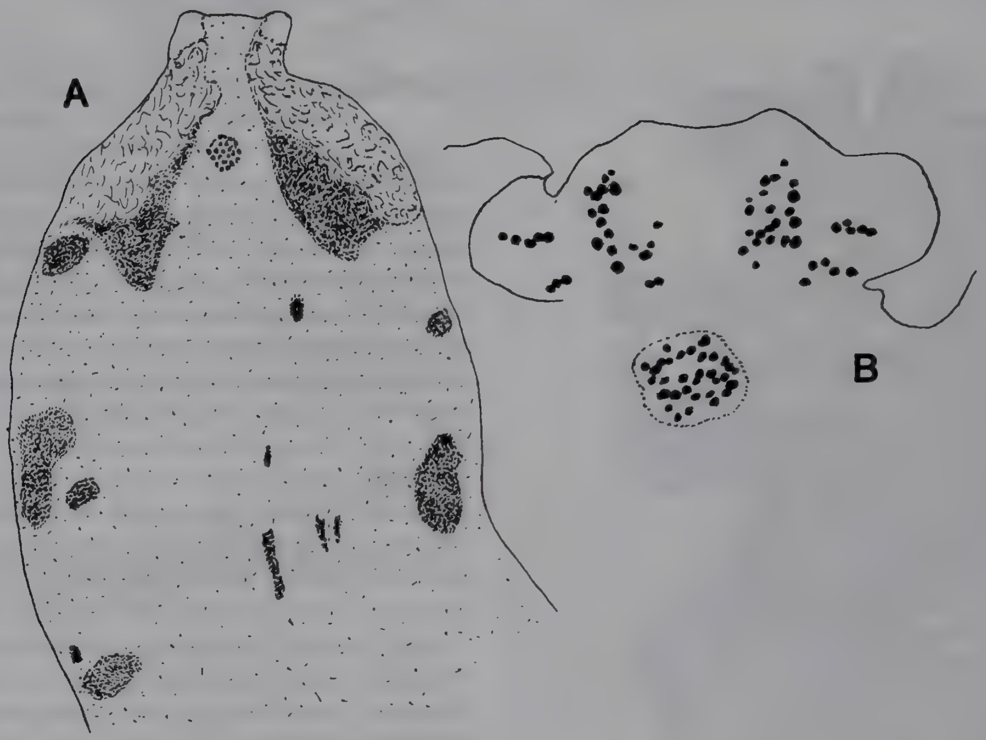

Fig.28. *Pseudoceros fuscomaculatus*: A, anterior half of body in life (dorsal view); B, arrangement of eyes.

DESCRIPTION (Fig.27). Three preserved specimens and a water-colour painting of this species are available. The painting is of an elongate-oval polyclad about 100 mm long and up to 60 mm wide. Its dorsal surface is reddish brown with numerous narrow yellow lines slanting postero-laterally from median line to margin of body (Fig.26A). Along the margin there is an irregular double row of black speckles. Ventral surface pinkish with black marginal band. Tentacles prominent, blackish, tipped with white.

When preserved, the body is oval and measures up to 40 mm long and 24 mm wide. Its ground-colour is greenish yellow dorsally and includes numerous thin white lines, faintly visible under magnification, which curve towards the median line where they terminate. Posterior to the intestinal trunk, the lines are not interrupted in median line and curve from one side of body to other, as shown in Fig.26C. A broad dark marginal band around body contains three whitish lines, except in the tentacular region where the band is wide and bears up to six white lines. These lines seldom link up with one another. Ventral surface of body whitish, with a plain brown narrow marginal band.

Margin tentacles deep brown and much folded, thus obscuring the disposition of tentacular eyes; about 60 cerebral eyes in a bluntly conical group (Fig.26B). Pharynx with about 10 pairs of lateral folds and relatively more elongate than is usual in *Pseudoceros*; intestinal trunk extends to near posterior region of body; it is without distinct lateral limbs, but gives off on either side a close network of narrow branches. The epidermis over the intestinal trunk is a little darker than the remainder of the body dorsally and this darkened area is edged with brown. Two male genital pores symmetrically disposed near posterior end of pharynx. Worthy of note is the apparent difference in the markings of the living worm from those of the preserved specimens cleared in methyl salicylate.

Pseudoceros fuscomaculatus sp.nov.

LOCALITY. In 24 metres, SE Glorieuses (11°32′S, 47°23′E), Benthedi, Comoro Is., 12.4.1947 (P. Bouchet *leg.*) B.M.reg. no. 1984.10.16.9–11 (syntypes).

DESCRIPTION (Fig.28). The living worms were elongate oval, but in the preserved condition the body is more rounded and the largest specimen measures about 5 mm long and 3 mm wide. All three specimen available are, however, immature.

Dorsal surface of body whitish with faint patches of tiny greenish dots. In the marginal regions of the body there are 12–16 irregular patches of greenish brown, with a few similarly coloured smaller patches scattered over the body. There is also a pair of symmetrically-disposed areas of dark green anteriorly. Ventral surface greenish, with a narrow marginal band of white. Tentacles mere dorsal folds of anterior margin of body containing few eyes. About 30 cerebral eyes in a rounded cluster dorsal to rounded cerebral organ.

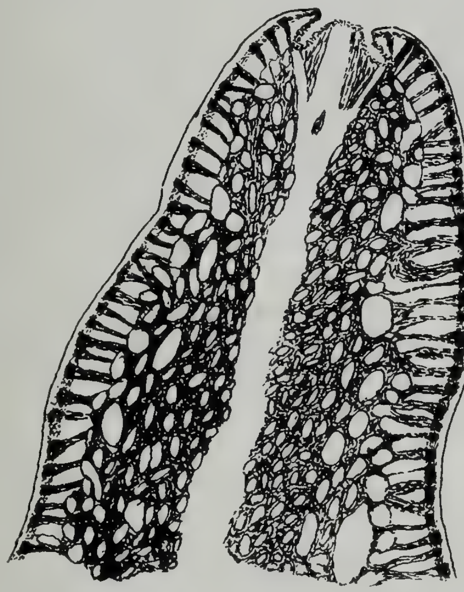

Fig.29 *Pseudoceros fuscoreticulatus*, anterior region of body in life (dorsal view).

Pseudoceros fuscoreticulatus sp.nov.

LOCALITY. Low tide, west coast, Inhaca I., Mozambique, July, 1958 (V. Gabie *leg.*) B.M.reg.no. 1985.7.5.26 (holotype).

DESCRIPTION (Fig.29). The single specimen available was, when alive, elongate oval, measuring about 30 mm long and up to 10 mm wide. A water-colour painting of the living worm shows the dorsal surface to have had a light brown ground-colour bearing a reticulum of dark brown. A median band is free of reticulation, except for two or three small patches. The areolae of the reticulum are small alongside the median band, but gradually enlarge towards the lateral margins of the body. The periphery of the body bears a thin band of yellow enclosing a band of blue. Marginally, the reticulum tends to end in fingers which overlap the blue band to affect blocks of black regularly disposed along the band.

A pair of tentacles appear as mere folds of the anterior margin of the body and bear the blue band of the body. In the preserved condition, the worm has lost coloration and pattern, and its tentacles are not distinct, having been much flattened at fixation. The flattening of the body has disarranged the tentacular eyes, and the cerebral eyes have been broken into a small mass of irregular fragments. Ventral sucker appears as a small depression situated a little anteriorly to middle of body. Initial stages in the development of the copulatory organs are apparent and show a single male complex.

Pseudoceros glaucus sp.nov.

LOCALITY. Coral reef, west shore, Inhaca I., Mozambique, 20.7.1962 (V. Gabie *leg.*); B.M.reg.no. 1985.7.5.27 (holotype).

DESCRIPTION. A water-colour painting shows the living worm to be about 35 mm long and up to 16 mm wide. Body-margin deeply folded. Dorsal surface of body bluish grey, with black maculae distributed over the body, except in marginal zones. There is also a median band speckled with black and grey. Marginal tentacles elongate and blackish. After preservation in alcohol, the specimen bears no resemblance to the painting, for its dorsal surface is brownish with a narrow light brown median band and a light brown marginal band. Ventral surface greyish. Tentacles in this specimen appear as distorted folds of the anterior body-margin, but they hold numerous eyes; about 35 cerebral eyes are arranged in a conical cluster. Pharynx with four pairs of deep lateral folds, each of which appear bifurcated and inclined posteriorly.

Single male genital pore lies between hinder pair of pharyngeal folds. Oval seminal vesicle about six times larger than globular prostate, but this considerable difference might be due to excessive flattening of the body at fixation; penis-stylet strong. Female pore midway between male pore and ventral sucker.

Pseudoceros gravieri Meixner, 1907

LOCALITY. Among seaweeds in about 6 metres opposite the Ambouti Stream, near Djibouti, Gulf of Tadjourrah, Djibouti.

DESCRIPTION. Meixner, 1907:468.

Pseudoceros inhacensis sp.nov.

LOCALITY. Inhaca I., Mozambique. (Holotype from opposite Marine Biol. Station, 20.7.1962—B.M.reg.no.1985.7.5.28; paratype among coral debris, west shore, 21.7.1963—B.M. reg.no. 1985.7.5.29).

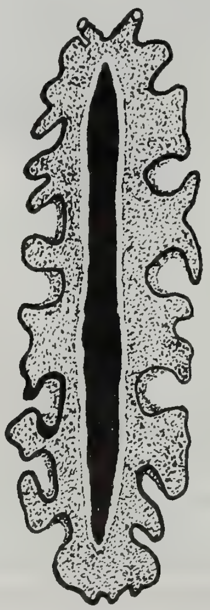

Fig.30 *Pseudoceros inhacensis*, dorsal surface of body in life.

DESCRIPTION (Fig.30). The holotype specimen is elongate oval with deeply notched margins. It measures about 40 mm long and 15 mm wide. Dorsally, the specimen is grey, faintly tinged with yellow and having a narrow black marginal band. Along the median line there is a wide band of deep brown tapering at both ends. Ventral surface greyish, but lighter than the dorsal surface. Anterior marginal tentacles well defined and with black borders. Male copulatory complex not apparent.

A variety of this species (paratype) 'was damaged when fixing' and is not available for study, but a water-colour painting (Fig.30) shows the worm to be similar in outline to that of the holotype specimen. It was about 70 mm in length and about 30 mm in maximum width. The dorsal coloration of this specimen was greyish with dull yellow patches. The body margin also carried a narrow black band. There was also a dark median band tapering towards its extremities. This band had a narrow reddish stripe, anteriorly fading to pale red bordered by black.

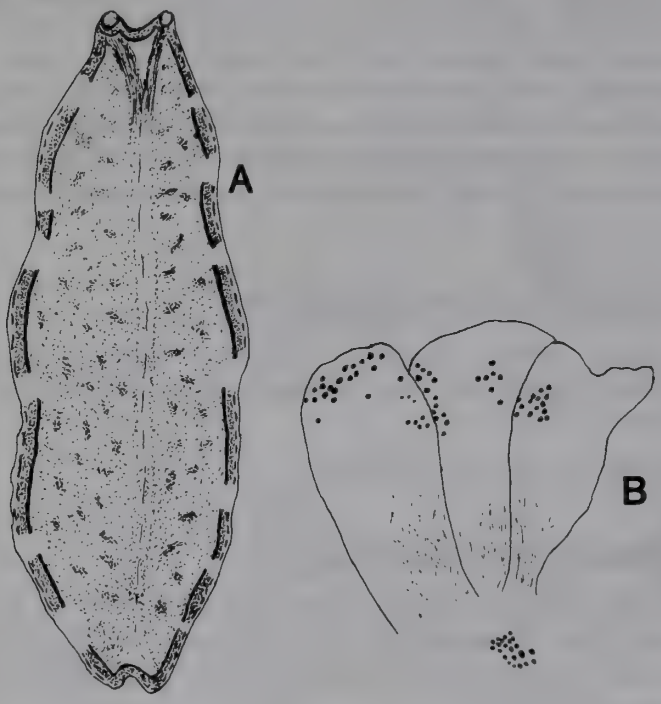

Fig.31 *Pseudoceros interruptus*: A, dorsal surface of body in life; B, cephalic region of body (dorsal view).

Pseudoceros interruptus (Stimpson, 1855) Kato, 1944

Eurylepta interrupta Stimpson, 1955

LOCALITY. In front of Marine Biol.Stat., Inhaca I., Mozambique, July, 1958 (V. Gabie *leg.*).

DESCRIPTION (Fig.31). Of this species only one specimen is available. It was fixed in Susa and 'measured 2.1 cm., stretched before fixation'. In the preserved state, it is oval in outline and measures about 16 mm in length and 10 mm in maximum width. Its ground-colour is brownish, with two dark irregular marginal bands dorsally and well separated from each other. A water-colour painting of the living worm shows the body to be elongate-oval in outline and the dorsal surface to be brownish with narrow streaks and small blotches of reddish brown. There is also a median band of grey enclosing a line of black streaks. There are also four marginal bands, the outer being white, bordering a narrow black line, which surrounds a distinct band of orange colour, with fourth or inner band of black. These marginal bands are broken at intervals by patches of white. Cerebral and tentacular eye-clusters as shown in Fig.31. Pharynx with five pairs of deep lateral folds.

Male pore immediately posterior to pharynx and leads into a male copulatory complex bearing a penis-stylet and appears to have no features to distinguish it from other species of *Pseudoceros*. Female pore at about 1 mm posterior to male; uterine canals extend from vagina to a little posteriorly to middle of body and give off a few lateral branches which anastomose.

NOTE. *Pseudoceros interruptus* has not previously been recorded since it was originally described by Stimpson from 'littoral, under stones in sandy places, near island of Loo Choo' [Okinawa], Japan. That the present specimen bears a very strong resemblance to the Japanese form may be seen from a composite of the descriptions of Stimpson (1855 & 1857), which runs as follows: oval, of a pale brown colour, with a median line of black blotches; margins ornamented with bands of dark brown, orange, black and an outer of white concentrically arranged and interrupted at intervals all round. Tentacles prominent, marginal; cerebral eyes in two crescents, convex forward, one behind the other; length ¾ inch. While the present specimen appears to differ slightly in coloration from the Japanese specimen, the pattern of markings in both specimens is very similar. The difference in the cerebral eye-clusters is undoubtedly due to fixation which very often alters the shape of the cerebral eye-clusters among species of *Pseudoceros*.

Pseudoceros kelaartii (Collingwood, 1876) Laidlaw, 1903

Eurylepta kelaartii Collingwood, 1876
Prostheceraeus kelaartii (Collingwood) Lang, 1882

LOCALITY. In 15–20 metres (12°45'S, 45°18'E), N.Ile Pamanzi, Mayotte, Comoro Is, 25.3.1977 (P. Bouchet *leg.*) Previously recorded from under stones in Singapore Harbour (Collingwood).

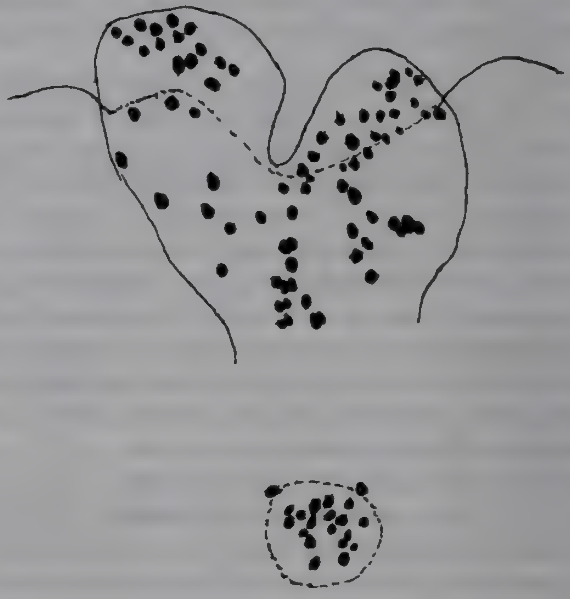

Fig.32 *Pseudoceros kelaartii*, Cephalic region of body (dorsal view).

DESCRIPTION (Fig.32). The preserved specimen available is elongate oval, 10 mm in length and 7 mm in maximum width. According to a colour transparency of the living worm, its dorsal surface is reddish or lilac-coloured and marked with elongate patches of white in the median and sublateral fields. This coloration and pattern closely resembles the coloured figure of *Eurylepta kelaartii* given by Collingwood. The white patches in the present specimen are, however, more numerous. Tentacles small, but distinct, each holding 30–40 eyes. About 18 eyes in group over cerebral organ. A pair of eyes lies on the antero-lateral borders of the cerebral organ and deeper in the parenchyma than the main group of cerebral eyes. The occurrence of a pair of precerebral eyes often appear among cotyleans, particularly among prosthiostomids, but it is doubtful whether their presence or absence is of diagnostic importance, because they may or may not be present in individuals of the same species. Mouth at about 0.7 mm posteriorly to cerebral organ and opening into anterior half of pharyngeal chamber; pharynx about 2.2 mm long and has five pairs of deep lateral folds. Ventral sucker 5.5 mm from anterior margin of body.

Male and female genital pores 0.5 mm apart and ventral to hind region of pharynx. With strong penis-stylet. Uterus formed by a pair of posteriorly-directed branching limbs, each of which gives off an antero-lateral branch to form a H-shaped figure.

Pseudoceros limbatus **(Leuckart, 1828) Lang, 1884**

Planaria limbata Leuckart, 1828

Localities. Red Sea (Leuckart, 1828). Among coral debris on west shore of Inhaca I., Mozambique, 21.7.1962 (V. Gabie *leg.*).

Description. Leuckart, 1828:11–15; Lang, 1884:544. Only a water-colour painting is available to the writer. This specimen, when alive, was elongate oval and measured 40 mm in length. Dorsally, its ground-colour was light grey, bordered by a narrow band of black. There was also on the dorsal surface a broad median longitudinal band of dark reddish brown, not reaching to ends of body. Ventral sucker light grey.

Note. The painted worm differs from Leuckart's description inasmuch as the ground-colour of the original specimen was pale green and the margins whitish, bordering a somewhat thicker band of black. Moreover, Leuckart's specimen appears, in his figure, to have had a median blood-red band. Investigation of further material from Inhaca I. might reveal that there is really no specific difference between this species and *Pseudoceros inhacensis* n.sp.

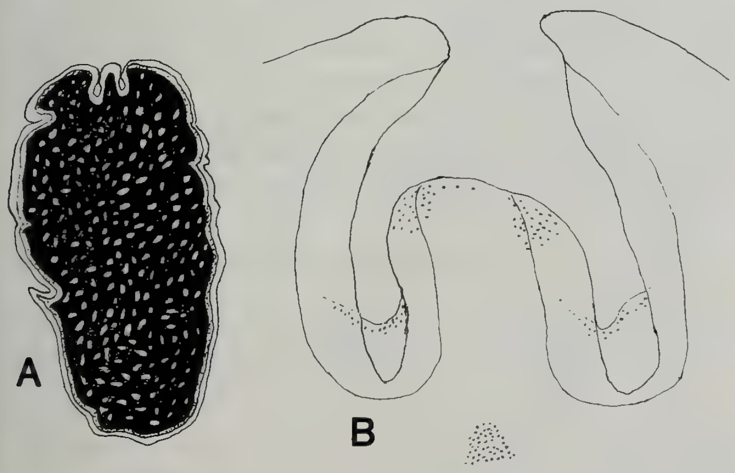

Fig.33 *Pseudoceros microcelis*: A, dorsal surface of body in life; B, cephalic region of body (dorsal view).

Pseudoceros microcelis **sp.nov.**

Locality. Opposite Marine Biol.Station, Inhaca I., Mozambique, May, 1965 (V. Gabie *leg.*) B.M.reg.no. 1985.7.5.32 (holotype).

Description (Fig.33). The only specimen available is much flattened and measures 35 mm in length and 23 mm in maximum width, whereas when alive it was about 55 mm long and 35 mm wide. A water-colour painting of the living worm shows the ground-colour of the dorsal surface to be black, adorned with numerous yellow spots of various shapes and sizes, bordered by a narrow band of yellow enclosing a narrow band of grey. All coloration and markings have been lost in the preserved specimen. Ventral sucker centrally situated. Tentacular and cerebral eye-clusters as depicted in Fig.33, and are the smallest the writer has so far met with in the genus *Pseudoceros*.

Single male copulatory complex lies adjacent to hind end of phaynx and receives vasa deferentia which arise near level of ventral sucker. The remaining features of the male and female complexes are obscured, owing to excessive flattening at fixation.

Despite the paucity of specific information, the present species may be readily recognized by the pattern of coloration on the dorsal surface of the body and by the relatively tiny cerebral and tentacular eyes.

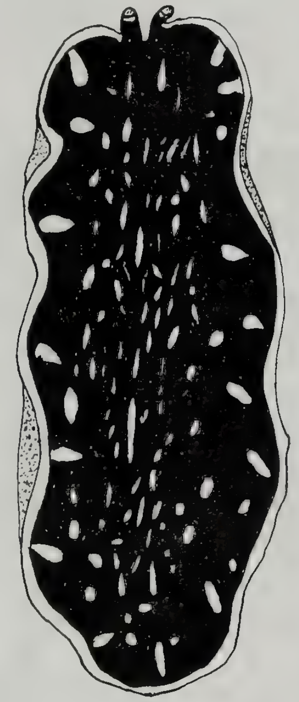

Fig.34 *Pseudoceros mossambicus*, dorsal surface of body in life.

Pseudoceros mossambicus **sp.nov.**

Locality. In front of Marine Biol. Stat., Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*) B.M.reg.no. 1985.7.5.33 (holotype).

Description (Fig.34). The only specimen available is oval in outline and measures 65 mm in length and 30 mm in maximum width. According to a water-colour painting of the living worm, its dorsal surface is black with many greenish yellow maculae of differing shape and size, as shown in Fig.34. There is a marginal band of orange, which also occurs on the tips of the marginal tentacles. Ventral surface of body ash-grey.

Owing to dense coloration, it has not been possible, even after clearing in methyl salicylate, to make out the disposition of tentacular eyes, but there appear to be about 70 cerebral eyes arranged in a conical cluster. Pharynx thrown into five pairs of deep lateral folds, the hinder pair almost embracing

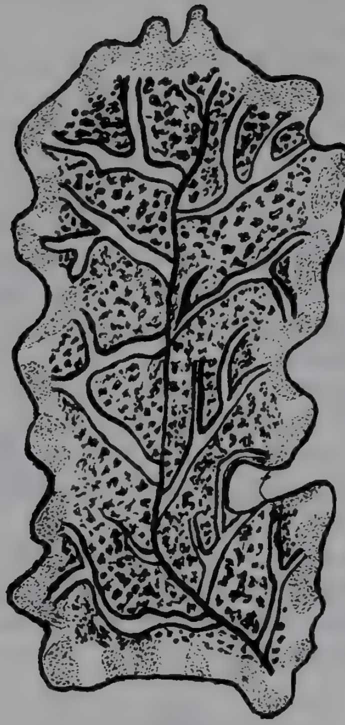

Fig.35 *Pseudoceros nigriramulosus*, dorsal surface of body in life.

the male copulatory complex which appears to have no specifically diagnostic features. A pair of moniliform uterine canals extend posteriorly from the female complex to a little beyond middle of body, but show no evidence of branching.

Pseudoceros nigriramulosus sp.nov.

LOCALITY. Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*) B.M.reg.no.1985.7.5.34 (painting).

DESCRIPTION (Fig.35). No specimen available, but according to a water-colour painting the living worm is elongate oval, about 32 mm long and 16 mm wide. The ground-colour of its dorsal surface is yellow with a thin black marginal band around the body. A black median line extends from anterior to posterior region of body, giving off lateral limbs along its course. These limbs have secondary branches. The areas between the branches are speckled with black. There is a yellowish submarginal band with red blotches disposed intermittently along the band. Red blotches also cover marginal tentacles.

Pseudoceros ovimaculatus sp.nov.

LOCALITY. Opposite Marine Biol.Stat., Inhaca I., Mozambique (V. Gabie *leg.*) B.M.reg.no. 1985.7.8.1 (holotype).

DESCRIPTION (Fig.36). The living worm according to a water-colour painting is broadly oval and measures about 20 mm in length. Its marginal tentacles are prominent and deep brown. Dorsal surface of body brownish, deeper in median region, lighter towards margins; brownish surface furnished with many white oval maculae. An elongate area between tentacles of a lighter brown than remainder of dorsal surface. Ventrally, body pinkish.

Unfortunately, the only preserved specimen available has been much flattened and is fragmentary. However, sufficient detail has been made out to mention the following; between fifty and sixty eyes in each retracted tentacle; cerebral eyes in two clusters, as shown in Fig.36. Pharynx with four pairs of deep lateral folds. Single male copulatory complex badly damaged; female complex typical of the genus, with dilated 'shell'-chamber dorso-ventrally compressed. Uterine canals show signs of forming a network.

Pseudoceros papilionis (Kelaart, 1858) Lang, 1884

Planaria papilionis Kelaart, 1858
Acanthozoon papilio (Kelaart) Collingwood, 1876
Pseudoceros papilio (Kelaart) Lang, 1884
Prostheceraeus papilio (Kelaart) Kaburaki, 1923

LOCALITY. Under stones at St James, False Bay, Cape Province, South Africa (Palombi, 1938:355). Recorded also

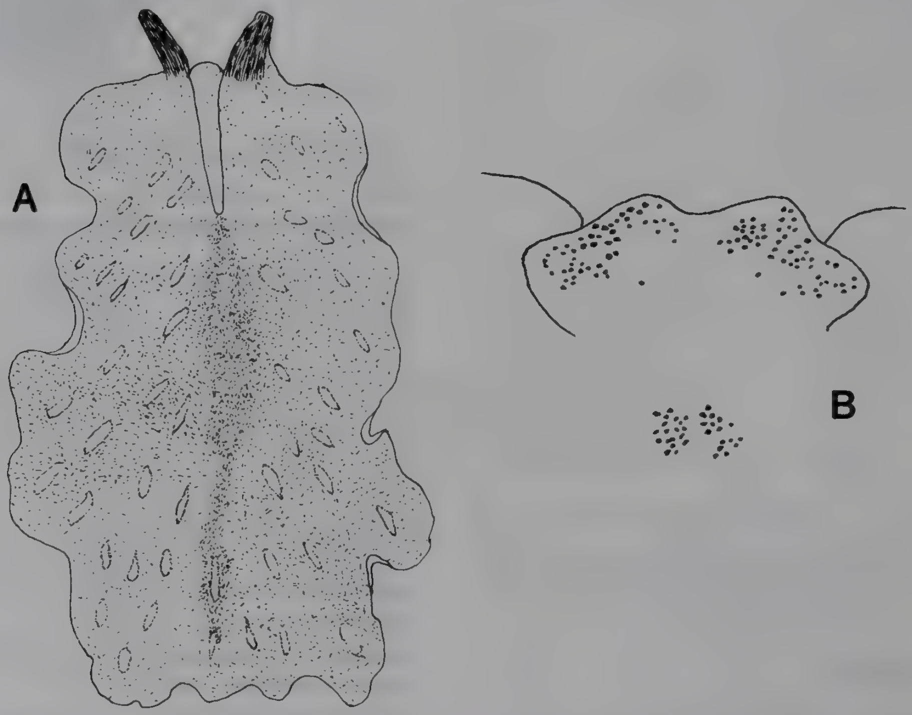

Fig.36 *Pseudoceros ovimaculatus*: A, dorsal surface of body in life; B, arrangement of eyes.

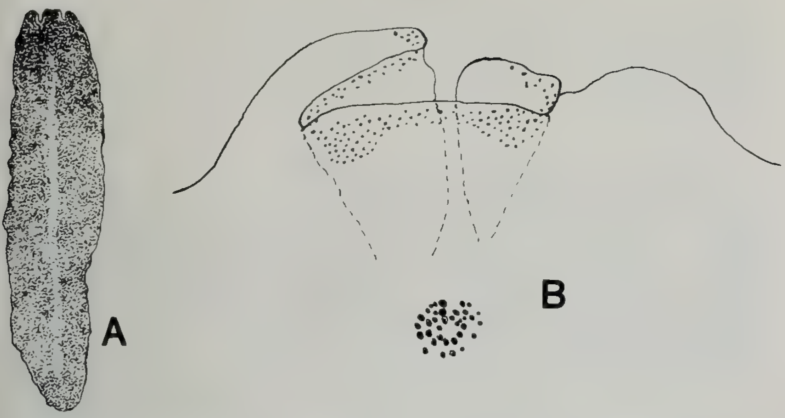

Fig.37 *Pseudoceros perviolaceus*: A, dorsal surface of body in life; B, arrangement of eyes.

from Sri Lanka (Kelaart, 1858) and Philippines (Kaburaki, 1923).

Descriptions. Kelaart, 1858:136; Collingwood, 1876:95; Kaburaki, 1923:646.

Pseudoceros perviolaceus Hyman, 1959

Eurylepta violacea Schmarda 1859, *nec* Collingwood, 1876
Proceros violaceus (Schmarda) Diesing, 1862
Pseudoceros velutinus (Blanchard, 1845), var. *violaceus* (Schmarda) Lang, 1884
Pseudoceros violaceus (Schmarda) Stummer-Traunfels, 1933

Locality. Low tide on sand-flats and among coral fragments on west coast and in front of Marine Biol.Stat., Inhaca I., Mozambique (V. Gabie *leg.*) This species has also been recorded from east and west coasts of Sri Lanka (Schmarda, 1859), Red Sea (Boutan, 1892) and Palau Is (Hyman, 1959).

Descriptions (Fig.37). Lang, 1884:540; Stummer-Traunfels, 1933: 3544; Hyman, 1959*a*:566; Hyman, 1959*b*:7. Three preserved, much flattened specimens from Inhaca I. are available. They are elongate, measuring up to 40 mm long and 25 mm wide, but they may be four times longer than wide. The preserved worms are brownish, but when alive, as seen in a water-colour painting, the colour ranged from violet to deep purple, with a lighter median line dorsal to the intestinal trunk. Colour lighter ventrally. Arrangement of tentacular and cerebral eye-clusters as shown in Fig.37. Pharynx with four pairs of deep lateral folds; hind pair may bifurcate and almost enclose the single male complex bearing a penis-stylet.

Pseudoceros splendidus Stummer-Traunfels, 1933

Pseudoceros superbus Lang, 1884, *nec*. Schmarda, 1859
Pseudobiceros splendidus (Stummer-Traunfels) Faubel, 1984

Locality. In front of Marine Biol. Stat., Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*). This species appears to be widely distributed having been recorded from the Mediterranean, Vietnam, Galapagos Is., Puerto Rico and Bermuda.

Description. Lang, 1884:540. The body measures up to more than 60 mm long and 30 mm wide. In the living worm, the dorsal surface is deep bluish or purplish black, with a velvety appearance, bordered all round with a narrow submarginal band of white or orange-yellow, enclosed by a marginal band of blue-black or purplish brown. The orange-yellow band follows the anterior tentacular folds to their tips, but on the inner margin of the folds and between their bases it is absent. When preserved in alcohol, the body becomes brown and sometimes shows a pale narrow submarginal band. There is also a dark band on the median line. Ventral sucker centrally placed or somewhat anterior to middle of body. With paired male copulatory complexes, each with a penis-stylet.

Pseudoceros tristriatus Hyman, 1959

Locality. In front of Marine Biol.Stat., Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*) Known also from the Caroline Is and Indonesia (Hyman, 1959*b*).

Description (Fig.38). Hyman, 1959*a*:576. The type-specimen of this species from the Ifaluk Atoll, in the western Caroline Islands is immature. In the preserved state it is, according to Hyman, entirely black, but from a colour-photograph of the worm in life, the ground-colour of the dorsal surface was light blue with three longitudinal orange-coloured bands. These bands were faintly bordered with black and extend from close behind the tentacles to near the posterior end of the body. The two lateral bands were confluent posteriorly to the median band.

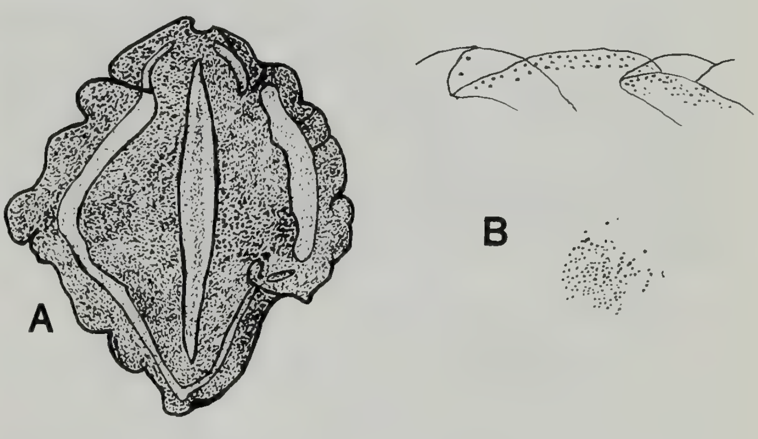

Fig.38. *Pseudoceros tristriatus*: A, dorsal surface of body in life; B, arrangement of eyes.

In a water-colour painting of the live specimen from Inhaca I., the dorsal pattern of markings is similar to that seen in Hyman's colour-photograph in having three longitudinal orange bands, with the laterals being confluent posteriorly to the median band. Dorsally, the ground-colour of this specimen was mauve and a band of deep blue bordered the body as well as the orange longitudinal bands, but these features are now lost in the preserved specimen. The living worm was about 48 mm long and 44 mm wide.

Anterior marginal tentacles are indistinct in both the painting and the preserved specimen. Tentacular eyes relatively few, and cerebral eyes in an irregular mass of about 100. Pharynx with five pairs of deep lateral folds curving posteriorly; intestinal trunk with numerous short lateral limbs that open into a dense network of intestinal branches.

Male genital pore lies between posterior pair of pharyngeal folds. Male copulatory complex well developed; prostate small and globular; seminal vesicle relatively large and pyriform; penis-papilla with stylet.

Note. The pattern of dorsal bands in *Pseudoceros gratus* Kato, 1937, from Japan and Western Australia is similar to

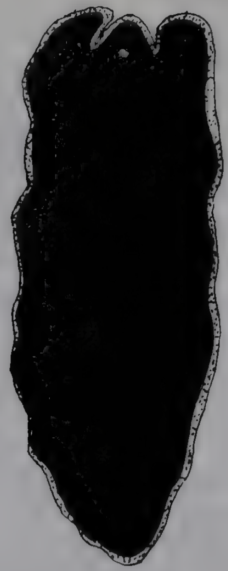

Fig.39 *Pseudoceros velutinus*, dorsal surface of body in life.

that found in the specimen from Inhaca I. Dorsally, the ground-colour of the Japanese form is, however, milky white with three black bands disposed as in *P. tristriatus* and with a black band around the body. This close resemblance in the disposition of markings in three forms from widely-separated areas, suggests that the importance of coloration in species of *Pseudoceros*, as implied by its numerous species known only on one specimen, might not be so diagnostically valuable for specific determination. Another point of interest is that *Pseudoceros tristriatus* has only one male copulatory complex, whereas *P. gratus* has two, again casting suspicion on the validity of considering the number of male complexes as a diagnostic feature among species of *Pseudoceros*.

Pseudoceros variegatus sp.nov.

Locality. Opposite Marine Biol. Stat., Inhaca I., Mozambique, 11 July 1961 (V. Gabie *leg.*)

Description. No specimen available, but a water-colour painting of the living worm, shows the body to be broadly oval and measuring about 25 mm long and 20 mm wide. According to the painting, the ground-colour of the dorsal surface is reddish brown, with a thin marginal band of dark brown around the body. This surface also bears pale pink elongate patches and a median whitish band extending for almost the length of the body. Ventral surface pinkish. No further information available.

Pseudoceros velutinus (Blanchard, 1847) Lang, 1884

Proceros velutinus Blanchard, 1847

Locality. In front of Marine Biol.Stat., Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*); Kabret, Suez Canal (Palombi, 1928). Recorded also from the Mediterranean (Blanchard, 1847; Lang, 1884 (coloured fig.)) and surface waters of the Gulf Stream.

Description (Fig.39). Lang, 1884,538. The specimen from Inhaca I. is shrivelled, presumably having dried up at some time and is useless for diagnostic purposes. There is, however, a water-colour painting of this specimen when alive. It appears to have been elongate oval and measuring 17 mm long, although the species is known to reach a length of 50 mm. The dorsal surface is velvety bluish black with a marginal band of purple and has a small colourless area over the rounded cluster of cerebral eyes. This colourless area appears to be specific.

Pseudoceros vinosus Meixner, 1907

Locality. Entedebir, Eritrea, March 1962 (from H. Steinitz colln.) Originally recorded from under stones in shallow water near Obock on the Clochetterie Reef in Gulf of Tadjourrah, Djibouti (Meixner, 1907).

Description. Meixner, 1907:470. Three specimens from Entedebir are available for study and agree well with the description given by Meixner. The original specimens were, when alive, wine-coloured and speckled with yellow and white. The present specimens preserved in alcohol are now whitish, but faint traces of red do occur. They are mature and measure 8–27 mm long. Tentacular eyes form a narrow band extending round and between the tentacles from the lateral base of one tentacle to the lateral base of the other; there are 50 or more cerebral eyes in a conical mass. Pharynx with 4 to 6 pairs of deep lateral folds, gradually becoming larger and longer posteriorly, so that the posterior pair almost envelop the copulatory complexes. Thin-walled seminal vesicle oval or pyriform, much larger than muscular globular prostate; penis-stylet long, lying in muscular penis-sheath. Uterine canals short, extending to level closely posterior to centrally-placed ventral sucker.

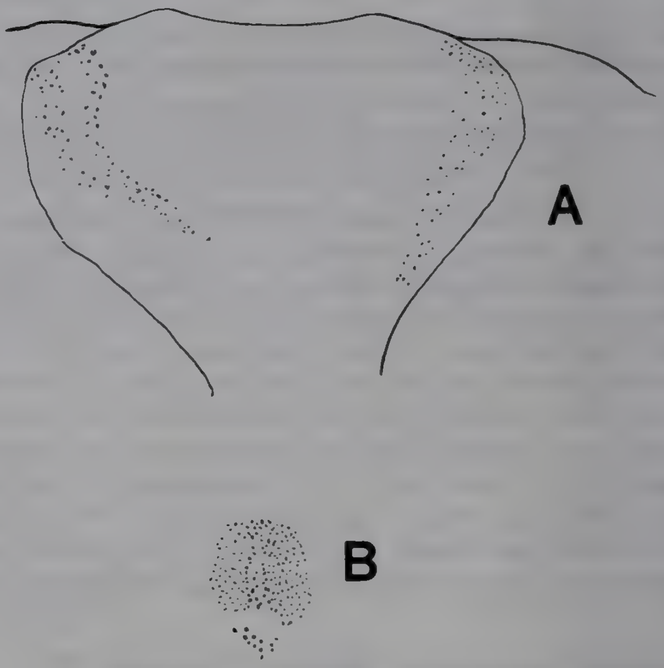

Fig.40 *Pseudoceros violaceus*: A, tentacles with eyes (dorsal view); B, arrangement cerebral eye-cluster (ventral view).

Pseudoceros violaceus (Kelaart, 1858) Hyman, 1959

Planaria violacea Kelaart, 1858
Eurylepta violacea Collingwood, 1876

Locality. On sand-flats, low tide, in front of Marine Biol. Stat., Inhaca I., Mozambique (V. Gabie *leg.*) Known hitherto only from Sri Lanka (Kelaart).

Description (Fig.40). Kelaart's description is brief and a coloured figure by him is published in Collingwood (1876).

The present specimens from Inhaca I. are up to 40 mm long and 15 mm wide. In a water-colour painting of the living worm, the ground-colour of dorsal surface is violet-purple with a narrow marginal band of yellow and a median band of yellow gradually fading at its sides into the dark ground-colour and tapering at both ends. Ventral surface lighter in colour and bears the yellow marginal band. Arrangement of eyes as shown in Fig.40. Pharynx with 4 or 5 pairs of deep lateral folds, the posterior of which may bifurcate. Single male genital pore; penis-papilla with stylet; seminal vesicle oval, much larger than the globular prostate. Uterine canals appear on either side of median line as a network of branches, becoming posteriorly confluent.

Pseudoceros zebra (Leuckart, 1828) Lang, 1884

Planaria zebra Leuckart, 1828
Pseudoceros pleurostictus Bock, 1913

LOCALITIES. On coral-reef, western shore of Inhaca I., Mozambique, 20.7.1962 (V. Gabie *leg.*) and Comoro Is, northern region of Mozambique Channel (P. Bouchet *leg.*); El Tor, Gulf of Suez (Leuckart); Macamby, Malagasy (Bock).

DESCRIPTIONS (Fig.41). Leuckart, 1828:11; Lang, 1884:546; Bock, 1913:257. This species appears variable in colour, but less so in markings. According to a water-colour painting, a living specimen from Inhaca Is. measured about 33 mm long and 10 mm wide. Its ground-colour was pale yellow, with a whitish median band and an orange-coloured marginal band. From the median band, transverse black bars, which may bifurcate or trifucate, reach the marginal band (Fig.41A). This specimen was much flattened at fixation and preserved in alcohol, and now measures 35 mm long and 18 mm wide. The black bars are still distinct, but the orange marginal band is much faded.

The marginal tentacles in the preserved specimen are so mutilated that it is not possible to make out the normal arrangement of the tentacular eyes, although there may be about 100 such eyes present; cerebral eyes number about 25 arranged in an elongate cluster (Fig.41B).

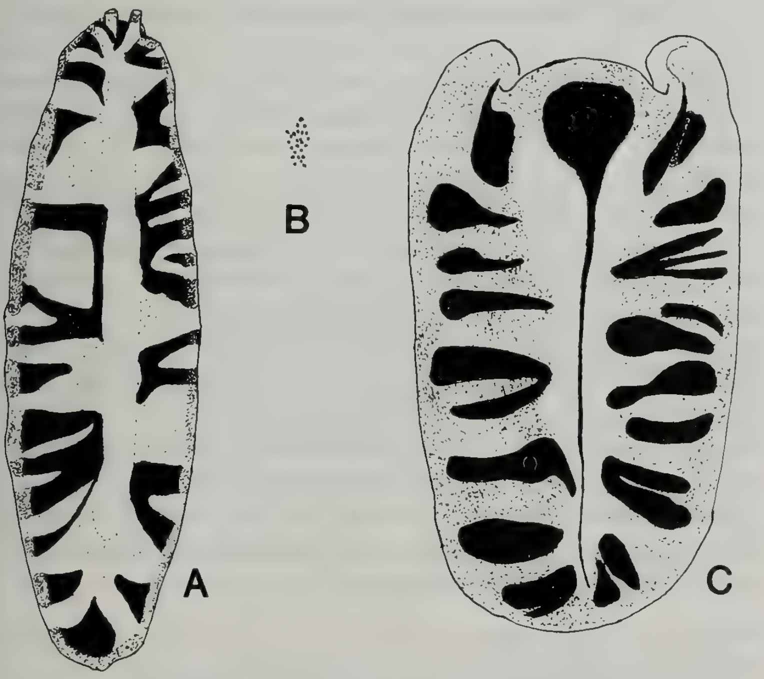

Fig.41 *Pseuceros zebra*: A, specimen from Inhaca I.; B, cerebral eyes of Inhaca specimen; C, specimen from Comoro Is.

Pharynx with five pairs of lateral folds, individuals of which may bifurcate, hinder pair relatively long and partially embrace the male copulatory complex. Owing to the excessive flattening of the specimen it has not been possible to interpret the morphology of the copulatory organs satisfactorily, but a penis-stylet has been detected.

An immature specimen from the northern waters of the Mozambique Channel appears to be a variant of the southern form. According to a colour-transparency, its dorsal surface is orange in the marginal and submarginal zones and yellowish in the median field. There are also black transverse blotches in each lateral field (Fig.41c). A large median black patch lies immediately posterior to the anterior marginal tentacles and from this a very thin black line extends to posterior end of body.

Genus *PARAPSEUDOCEROS* gen.nov.

DEFINITION. As *Pseudoceros*, but lacks tentacular eyes. With pair of precerebral ventral eyes.

TYPE-SPECIES. *Parapseudoceros dubius* sp.nov.

Parapseudoceros dubius sp.nov.

LOCALITY. In front of Marine Biol. Stat., Inhaca I., Mozambique, July 1958 (V. Gabie *leg.*) B.M.reg.nos. 1985.7.3.8 (holotype) and 1985.7.3.9 (paratype).

DESCRIPTION (Fig.42). This species is represented by two preserved specimens, both of which are in poor condition, having been excessively flattened to wafer thin at fixation and are now almost friable. Both specimens have, however, had their natural appearance recorded in a water-colour painting. Each is oval in outline, with a distinct median indentation on the anterior margin of the body. One living worm (holotype) was about 12 mm long and 6 mm wide. Its dorsal surface was blotched with colour varying from crimson to purple, with a darker median band, and irregularly mottled with a lighter colour. Ventral surface paler than the dorsal. The second worm (paratype) measured, when alive, about 18 mm long and 12 mm wide. Its dorsal surface was light brown, mottled with dark brown, and a pinkish median band in anterior half of body. The painting also indicates a pinkish under surface. Ventral sucker well developed in middle of body.

A pair of marginal tentacles appear as small humps on either side of a deep notch on the anterior margin of the

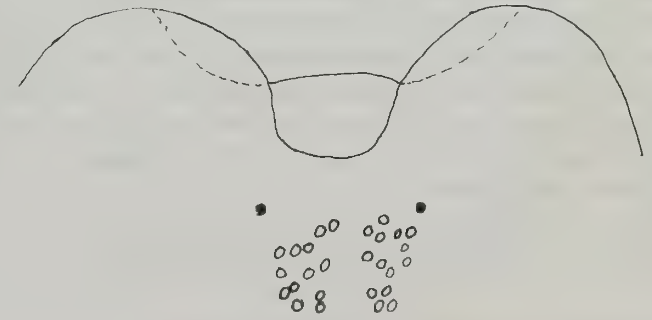

Fig.42 *Parapseudoceros dubius*, tentacular region of body with cerebral eyes.

body. No eyes have been detected in the tentacular region of both specimens. Cerebral eyes arranged in two approximate elongate clusters, with 13–17 eyes in each, lying dorsally to the cerebral organ. In one specimen (holotype) there is a single eye situated anteriorly and laterally to each cerebral cluster and deep in the parenchyma. In the other specimen, the latter eyes are less apparent, lying nearer to the clusters.

Pharynx closely posterior to cerebral eyes and thrown into 3 or 4 pairs of deep lateral folds; intestinal trunk extends to hind end of body and gives off a close network of canals.

Male copulatory complex adjacent to posterior pharyngeal folds. Its structure is typical of the genus *Pseudoceros*. Penis-papilla with strong stylet. Female genital pore near male pore; uterine canals form a close network. The coloration of the holotype closely resembles Collingwood's coloured figure of *Eurylepta kelaartii*, which has a pair of small approximate marginal tentacles. The anterior notch in the present specimens probably indicates the presence of a pair deeply retracted tentacles. The brownish form is very likely merely a colour variety.

NOTE. In its gross morphology the above-described form undoubtedly resembles that of the genus *Pseudoceros*, but the lack of tentacular eyes separates it from this genus. Whether this feature alone is of generic or subgeneric importance is questionable. A similar problem is, however, found in the genus *Licheniplana* Heath & McGregor, 1913, which appears to be identical with the pseudocerotid genus *Thysanozoon* Grube, 1840, but differs only in the absence of tentacular eyes. Modern authors appear to have accepted this difference as generically important. Therefore, to be consistent, a new genus *Parapseudoceros* has been erected for the present species.

Genus *THYSANOZOON* Grube, 1840

DIAGNOSTIC FEATURES. Dorsal surface of body bears numerous papillae, into which intestinal diverticula may extend. Male copulatory complex single or double, closely posterior to pharynx.

Thysanozoon brocchii (Risso, 1818) Grube, 1840

Tergipes brocchi [*sic*] Risso, 1818
Eolidiceros brocchii (Risso) Quatrefages, 1845

LOCALITIES. Port Said, Suez Canal, 13.12.1924 (Palombi, 1928); 13°N, 15.4°W., Baie de Caballo, Rio de Oro, west coast of Africa, 2.11.1935 (Palombi, 1939); Shelly Beach, East London, Cape Province, South Africa. (Palombi, 1939); Algeria (Dieuzeide & Goeau-Brissonniere, 1951); South Africa, Cape Province: (from intertidal rocks, Richmond, 25.3.1939); among rocks in 18 metres, off Gordons Bay, False Bay, 25.6.1952; Jefferies Bay, between Still Bay and Port Elizabeth. (Day colln.) Known also from the Mediterranean, Borneo, Japan, Florida, Vietnam, New Zealand, Brazil, Caribbean and England.

DESCRIPTIONS. Lang, 1884:525; Kaburaki, 1918:48.

Thysanozoon cruciatum Schmarda, 1859

Thysanozoon (*Eolidiceros*) *cruciatum* Schmarda, 1859
Thysanozoon brocchi var. *cruciatum* (Schmarda) Laidlaw, 1906.

LOCALITY. Cape Verde Is. (Laidlaw, 1906,713.) Originally described from Australia and New Zealand.

DESCRIPTIONS. Schmarda, 1859, 30; Lang, 1884, 526; Stummer-Traunfels, 1895, 714 and 1933, 3550.

Thysanozoon discoideum Schmarda, 1859

LOCALITIES. East London, Cape Province, Dec.1960 (V. Gabie *leg.*); Baui I., Tanzania (Stummer-Traunfels, 1895); Home Wood Beach, Port Elizabeth, Cape Province, South Africa (Palombi, 1938, 354). Originally described from Sri Lanka.

DESCRIPTIONS. Schmarda, 1859:29; Stummer-Traunfels, 1895:716.

Thysanozoon plehni Laidlaw, 1902

LOCALITY. Coral-reef, west shore of Inhaca I., Mozambique, 20.7.1962 (V. Gabie *leg.*) *T. plehni* originally described from Minikoi, Laccadive Is, Indian Ocean.

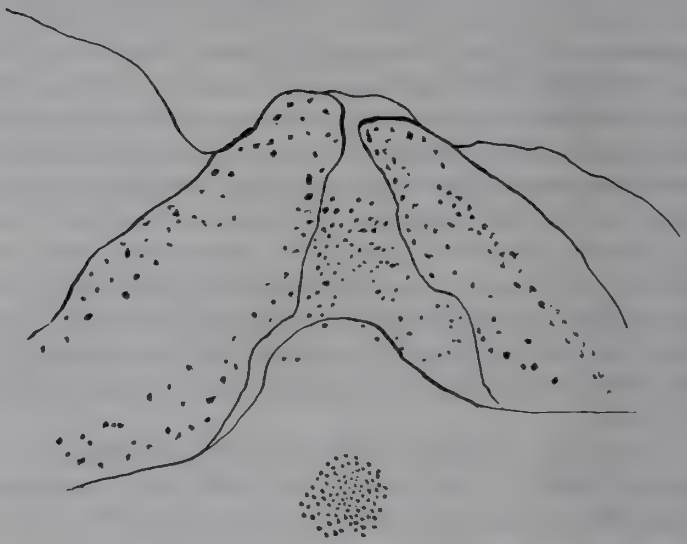

Fig.43 *Thysanozoon plehni*, tentacles and eye-clusters.

DESCRIPTION (Fig.43). Laidlaw, 1902:294. Two Inhaca specimens are available for study, one of which was the subject of a water-colour painting when alive. The other specimen is so fragmentary as to be of no use whatever. The painting shows the ground-colour of the dorsal surface of the body to be whitish and covered with numerous black papillae, which are concentrated above the median line and gradually becoming less numerous and smaller towards the margin of the body. Underlying gonads seen as small dark spots lying between the papillae, There is also a very narrow marginal band of deep pink. Body broadly oval, about 35 mm long and 30 mm wide. Marginal tentacles well developed and completely black. Single male genital pore. Male copulatory complex typically pseudocerotid in having no specifically diagnostic features, except perhaps a relatively long penis-stylet. Female copulatory complex again typical.

NOTE. In appearance, the above specimen resembles *Thysanozoon plehni* very closely. The ground-colour of Laidlaw's 'spirit specimen' is described as 'dull pale yellow'. Moreover, 'on the dorsal surface lie a considerable number of black, rather pointed papillae; the small marginal tentacles are also black.' The African specimen differs only in the ground-colour of the body and in the presence of a narrow marginal band of pink. Nevertheless, the difference in ground-colour is negligible and the marginal band in the living worm was probably lost in the preserved specimen. Laidlaw makes an interesting observation concerning *T. plehni* for he states that:

> 'Whereas the gonopore is situated on the middle line, the penis with the penis-sheath lies very decidedly to one side of it, the right side. But the cavity of the [male] antrum is extended fairly equally to the right and to the left of the middle line. This peculiarity perhaps indicates that this species is descended form a form in which, as in some other species of *Thysanozoon*, the penis is paired, and that one of the pair, the left in this instance has disappeared leaving the right penis to open into the side of the antrum.'

This observation strengthens the present writer's view, mentioned above under the genus *Pseudoceros*, concerning the apparent unreliability of recognizing the single or double copulatory complexes as diagnostic features among species of pseudocerotid genera.

Family **EURYLEPTIDAE** Stimpson, 1857

DIAGNOSTIC FEATURES. Body with smooth or papillate dorsal surface, which may be highly coloured. Pair of anterior marginal tentacles, sometimes difficult to detect. Ventral sucker well developed, in mid-third of body. Cerebral eyes in two elongate clusters; tentacular eyes within or at base of tentacles. Mouth at anterior end of short pharyngeal chamber near cerebral organ; pharynx tubular or bell-shaped, directed anteriorly; intestinal trunk extends posteriorly, provided with paired lateral branches usually anastomosing. Testes ventral; ovaries dorsal. Genital pores between mouth and ventral sucker. Male copulatory complex simple, central or immediately posterior to pharynx. Vasa deferentia run anteriorly from hind region of body to open into well-developed seminal vesicle. Prostate rather small, independent; penis-papilla anteriorly directed, often with stylet enclosed in penis-sheath. Vagina short and simple. 'Shell'-chamber dilated and dorsoventrally flattened. Uterine canals unbranched; open into proximal end of vagina and extend posteriorly to hind level of intestinal trunk; uterine vesicles may occur.

Key to euryleptid genera from African waters

1 Penis-stylet present 2
1′ Penis-stylet absent .... ***Laidlawia***

2 Intestinal branches terminating in marginal vesicles .... ***Cycloporus***
2′ Intestinal branches without terminal vesicles 3

3 Marginal tentacles lappet-like 4
3′ Marginal tentacles as small folds of body-margin or inconspicuous .... ***Stylostomum***

4 Lateral intestinal branches anastomosing . . . ***Prosthoceraeus***
4′ Lateral intestinal branches not anastomosing . . ***Oligocladus***

Genus ***PROSTHECERAEUS*** Schmarda, 1859

DIAGNOSTIC FEATURES. Elongate-oval forms with smooth dorsal surface, often strikingly marked. Well-developed marginal tentacles with numerous eyes between and at their bases. Cerebral eyes in two clusters above the cerebral organ. Campanulate pharynx short; intestinal trunk long, with several pairs of lateral branches forming an anastomosing system. Penis-papilla with stylet. Uterine canals united posteriorly with uterine vesicles.

Prostheceraeus rubropunctatus Lang, 1884

LOCALITY. From bottom of lighter, Cape Verde Is (Laidlaw, 1906).

DESCRIPTION. Lang, 1884:56.

Prostheceraeus flavomaculatus Graff, *in* Saville-Kent, 1893

LOCALITY. Glorieuses Is, Northern Mozambique Channel (P. Bouchet *leg.*)

DESCRIPTION. This worm is available to the present writer only in colour-transparencies of the living animal. According to these, the ground-colour of the dorsal surface of the body is bluish black, amply spotted with yellow and bearing a whitish marginal band. The ventral surface is also bluish black, but without yellow spots. The anterior marginal tentacles bear the dorsal ground-colour and the whitish marginal band. In the mid-line, closely posterior to the tentacles, there is a pyriform clear space, presumably covering the cerebral organ and its eye-cluster. Information on the type-specimen of this species from Thursday I. on the Australian Great Barrier Reef is available only in a coloured picture of the living worm. The dorsal surface of this specimen is greenish blue, mottled with irregularly-shaped orange-coloured spots. There is also a wide marginal band of blue on which occur patches of yellow.

Prostheceraeus boucheti sp.nov.

LOCALITY. In 25 metres, south barrier-reef (13°04′S, 45°09′E), Mayotte, Comoro Is, northern Mozambique Channel, 27.3.1977, and in 10–20 metres, north reef, Mayotte, (12°35′S, 45°05′E), 30.3.1977 (P. Bouchet *leg.*) B.M.reg.no. 1984.10.16.1–2.

DESCRIPTION (Fig.44). Two specimens of this species are available, but they are badly fragmented. The body is oval and appears to measure 3.5 to 5 mm long and 2 to 3 mm wide. According to colour-transparencies of these worms when alive, the dorsal surface has a brownish ground-colour and a thin transparent margin enclosing a narrow band of yellow or greenish yellow. At about the junction of the anterior and middle thirds of the body, a large yellow spot lies in the median line. From this spot, a median reddish band extends to near posterior end of body, while a much narrower reddish band proceeds anteriorly from the yellow spot to near cerebral eye-cluster. Both median bands lie in area distinctly lighter than the remaining ground-colour of the dorsal surface. Ventral sucker central. Marginal tentacles as large lappets deeply pigmented with black, containing eyes, with further eyes between tentacles. Cerebral eyes in irregular cluster in one specimen, but inclined to form two elongate groups in the other. Both specimens are juvenile.

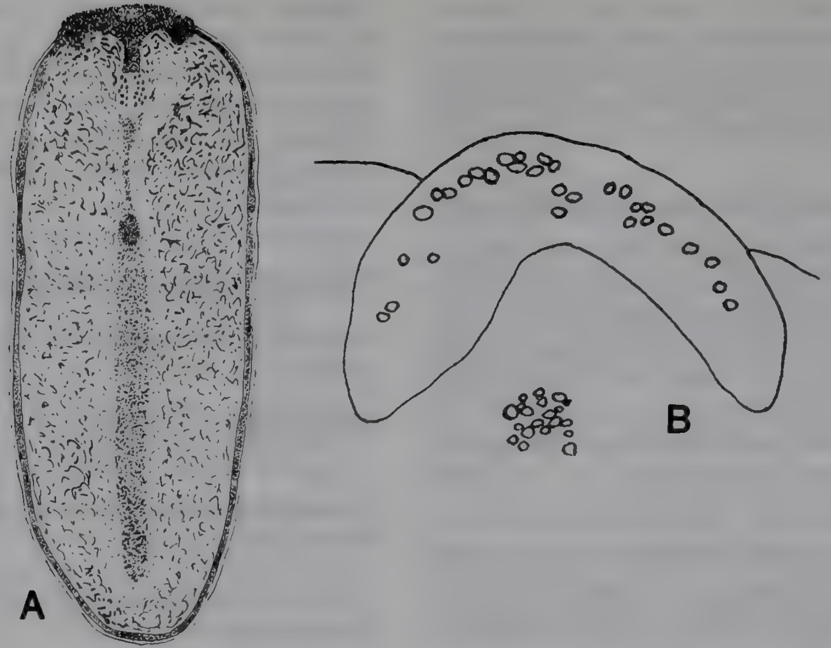

Fig.44 *Prosthecerαeus boucheti*: A, dorsal surface of body in life; B, tentacles and arrangement of eyes in preserved specimen.

Genus *CYCLOPORUS* Lang, 1884

Diagnostic features. Small oval forms with smooth or papillate dorsal surface. Small marginal tentacles with eyes in their bases and ventral surfaces. Cerebral eyes in two closely associated elongate clusters. Intestinal trunk extends to near posterior end of body, dividing into three branches anteriorly, median branch passing over cerebral organ; 6 to 10 pairs of lateral intestinal branches anastomose and terminate in small vesicles opening on margin of body. Vasa deferentia unite and immediately open into large seminal vesicle; prostate vertically disposed dorsally to male pore. Male antrum relatively deep; penis-papilla with stylet. Vagina narrow; uterine canals with vesicles.

Cycloporus papillosus (Sars, in Jensen, 1878) Bock, 1913

Thysanozoon papillosum Sars, in Jensen, 1878
Cycloporus papillosus Lang, 1884

Locality. Non-papillate form under stones at low tide, Porto Praya, Cape Verde Is (Laidlaw, 1906). Known also from Scandinavia, United Kingdom, NW France, Mediterranean and Vietnam.

Descriptions. Lang, 1884:568; Bock, 1913:262.

Genus *OLIGOCLADUS* Lang, 1884

Diagnostic features. Small oval forms with smooth dorsal surface. Pointed marginal tentacles, each with many eyes on ventral side. Cerebral eyes in two groups. Mouth anterior or ventral to cerebral organ; tubular pharynx well developed; intestinal trunk with 3 or 4 pairs of non-anastomosing lateral branches and extending to near posterior end of body, where it opens by a median dorsal pore. Male genital pore ventral to pharynx; vasa deferentia open independently into seminal vesicle lying dorso-posteriorly to male pore. Female genital complex ventral to hind region of pharyngeal chamber; uterine canals bear 1 to 4 pairs of vesicles.

Oligocladus sanguinolentus (Quatrefages, 1845) Lang, 1884

Proceros sanguinolentus Quatrefages, 1845

Locality. Among nodules of nullipores, dredged in 5 to 10 metres in St Vincent Harbour, Cape Verde Is (Laidlaw, 1906). Known also from Scandinavia, United Kingdom, NW France and Mediterranean.

Descriptions. Lang, 1884:580; Bock, 1913:267.

Genus *STYLOSTOMUM* Lang, 1884

Diagnostic features. Small elliptical forms, usually broader posteriorly. Tentacles small or inconspicuous. Cerebral and tentacular eye-clusters usually with few eyes. Mouth and genital pore may form a common antrum. Intestinal trunk with up to 6 pairs of lateral branches, which ramify and may anastomose. Male copulatory complex central or anterior to pharynx; with penis-stylet. Female complex ventral to hind region of pharynx; uterine canals form H-shaped figure with uterine vesicles.

Stylostomum ellipse (Dalyell, 1853) Lang, 1884

Locality. Near lighthouse, Cape Town, South Africa (Bock, 1913). Known also from Scandinavia, United Kingdom, Mediterranean, Falkland Is., South Georgia and Tierra del Fuego.

Descriptions. Lang, 1884:584; Bock, 1913:270.

Genus *LAIDLAWIA* Herzig, 1905

Diagnostic features. Small oval forms with inconspicuous marginal tentacles or difficult to make out. Eyes few. Intestinal trunk with 6 or 7 pairs of non-anastomosing lateral branches and an unpaired anterior branch. Penis-papilla in penis-sheath, but without stylet. Uterine canals unite posteriorly to form a large vesicle opening on dorsal surface of body. Posterior to female complex, uteri connected by transverse canal opening into genito-intestinal canal. Near opening of transverse connection, each uterine canal has a large vesicle.

Laidlawia polygenia Palombi, 1938

Locality. Under stones at Oudekraal, Cape Province, South Africa (Palombi).

Description. Palombi, 1938:360.

Family **PROSTHIOSTOMIDAE** Lang, 1884

Diagnostic features. Elongate or oval forms without tentacles. Ventral sucker usually present. Eyes marginal or submarginal, disposed anteriorly or in a continuous series round body; additional eyes in two elongate cerebral clusters or scattered fanwise anteriorly from cerebral organ. Mouth at anterior end of pharyngeal chamber, immediately posterior to cerebral organ. Muscular tubular pharynx directed anteriorly; intestinal trunk extends from pharynx to posterior region of body, with several pairs of non-anastomosing lateral branches. Genital pores separated, between pharynx and ventral sucker. Vasa deferentia originate in posterior half of body and extend anteriorly to open independently into a large muscular seminal vesicle lying between pair of accessory vesicles. Ejaculatory duct and ducts from accessory vesicles open into penis-papilla, bearing a strong stylet, in penis-sheath. Numerous unicellular glands open into lumen of penis-pocket. Vagina short, simple, looped anteriorly, without Lang's vesicle; 'shell'-chamber enlarged and dorsoventrally compressed. Uterine canals form H-shaped figure with transverse limb opening into proximal end of vagina.

Key to prosthiostomid genera from African waters

1 Muscular sheath enclosing male accessory vesicles .... ***Lurymure***
1′ Male accessory vesicles not enclosed in muscular sheath .... ***Prosthiostomum***

Genus ***PROSTHIOSTOMUM*** Quatrefages, 1845

Diagnostic features. Elongate or ribbon-like forms, broadly rounded or truncate anteriorly, gradually narrowing posteriorly. Cerebral eyes in one or two elongate clusters; marginal eyes variable, more often disposed in two or three irregular rows anteriorly. Intestinal trunk with unpaired anterior branch lying dorsally to pharynx. Male accessory vesicles not enclosed in muscular sheath.

Prosthiostomum capense Bock, 1931

Locality. Simon's Town, Cape Province, South Africa.

Description. Bock, 1931:296.

Prosthiostomum dohrnii Lang, 1884

Locality. Among nullipores at low tide and in about 18 metres, St Vincent Harbour, Cape Verde Is (Laidlaw, 1906). Known also from the Mediterranean.

Description. Lang, 1884:601.

Prosthiostomum siphunculus (delle Chiaje, 1828) Lang, 1884

Planaria siphunculus delle Chiaje, 1828.

Locality. Dredged in 20 metres off Meteor Reef, Gulf of Tadjourrah, Djibouti, 26.2.1904 (Meixner, 1907); Still Bay, Cape Province, South Africa, 5.1.1932 (Palombi, 1936); on algae, eastern harbour, Alexandria, Egypt (Steinböck, 1937); Port Etienne, Mauritania (de Beauchamp, 1951); known also from the Mediterranean, Black Sea, NW France, United Kingdom and Vietnam.

Description. Lang, 1884, 595; Palombi, 1936, 31; Lang, 1884, 595.

Prosthiostomum lineatum Meixner, 1907

Locality. On Porites, Musha I., Gulf of Tadjourrah, Djibouti.

Description. Meixner, 1907:482.

Prosthiostomum sp.innom. of Laidlaw (1906)

Locality. From nullipore on Bird Rock, St Vincent Harbour, Cape Verde I.

Description. Laidlaw, 1906:714.

Genus ***LURYMURE*** du Bois-Reymond Marcus & Marcus, 1968

Diagnostic feature. Differs from *Prosthiostomum* only in having the two male accessory vesicles bound in a muscular envelope.

Note. The validity of *Lurymure* as a genus appears to be uncertain. The present writer has found that in not fully developed specimens of *Prosthiostomum delicatum*, the accessory vesicles are quite independent of one another, but in fully mature specimens they are bound together by a muscular envelope. There is a suggestion of a similar condition in *Prosthiostomum purum*, as described by Kato (1937b). This gives rise to the question of whether or not *Lurymure* is really a late stage in the development of *Prosthiostomum*.

Lurymure delicatum (Palombi, 1939) du B.-R. Marcus & Marcus, 1968

Prosthiostomum delicatum Palombi, 1939

Localities. East London, Cape Province, South Africa, 25.7.1937 (Palombi). On vertical rock in 0–4 metres below LWST, Oatland Pt, False Bay; among rocks and stones in 9 metres, Algoa Bay, 6.4.1954; among rocks in 18 metres off Gordon's Bay False Bay 25.6.1952; in 7–9 metres, Fish Hoek Bay; on sandy bottom in 24 metres, 34°10′S, 18°27.5′E, False Bay; on rocks nr Seal I., False Bay, 22.2.1952—Cape Province, South Africa. (Day colln.)

Description. Palombi, 1939:135.

Note. In several specimens examined by the present writer and assigned to *L. delicatum* variations in the number of eyes are plainly visible. In the single specimen described by Palombi, there are 72 marginal eyes and 35 cerebral eyes, the latter divided into two groups, 17 in one and 18 in the other. In the present material, the number of marginal eyes varies from 35 to 110 and cerebral eyes 15 to 27 in each group. In most specimens their is a pair of precerebral ventral eyes, but in the remainder only one such eyes may be present. The specimen from off Gordon's Bay is said to have been 'pale fawn, blue eye-spots'.

Lurymure drygalskii **(Bock, 1931) du B.-R. Marcus & Marcus, 1968**

Prosthiostomum drygalskii Bock, 1931.

LOCALITIES. Cape Province, South Africa. (Simonstown Bay—Bock, 1931); (among coarse shell in 20 metres, Saldanha Bay; dredged on sand and shell substratum in 26 metres, 34°07'S, 18°36'E, False Bay, 30.2.1964—Day colln.); (Eylath, Gulf of Aqaba, 4.5.1955—H. Steinitz *leg.*).

DESCRIPTION (Fig.45). Bock, 1931:298.

NOTE. The main feature of this species is the small number and disposition of the cerebral eyes.

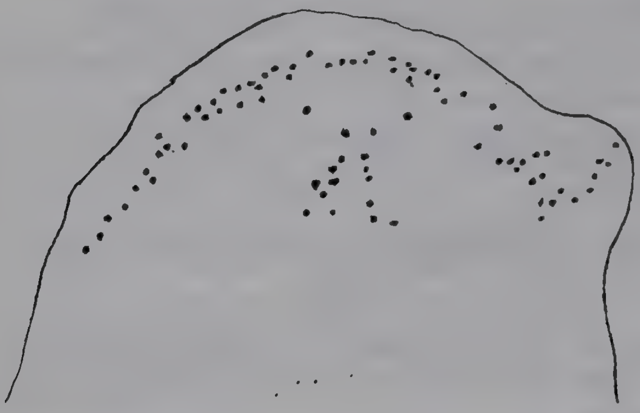

Fig.45 *Lurymure drygalskii*, arrangement of eyes.

Lurymure russoi **(Palombi, 1939) du B.-R. Marcus & Marcus, 1968**

Prosthiostomum russoi Palombi, 1939

LOCALITIES. Cape Province, South Africa. (Shelley Beach, East London—Palombi, 1939); ('on mixed bottom' in 4.5–5.5 metres below LWST., Oatland Pt., False Bay—Day colln.); on shell and rock in 42 metres, 25°57'S, 33°02'E., Mozambique —Day colln.).

DESCRIPTION. Palombi, 1939*a*:141.

NOTE. The large tubular pharynx appears to be the main feature of this species.

Prosthiostomum **(s.1.)** ***capense*** **Bock, 1931**

LOCALITY. Simonstown Bay, Cape Province, South Africa.

DESCRIPTION. Bock, 1913:296.

GLOSSARY

adhesive organ: muscular sucker, or adhesive pad or depression on ventral surface of body.

atrium: chamber receiving openings of two or more organ-systems.

bursa copulatrix: bulbous muscular organ opening into vagina externa.

cerebral organ or 'brain': a globular or bilobed mass of nerve-tissue in cephalic region of body.

cirrus: male copulatory organ capable of protruding (everting) by turning inside out.

cirrus-sac: cavity lined with hooks and spines which cover surface of cirrus when everted.

common sperm duct: canal uniting vasa deferentia with seminal vesicle.

ductus communis: duct formed by union of prostatic duct and ejaculatory duct.

ductus vaginalis: continuation of inner region of vagina after receiving uterine duct to open either to exterior or into vagina externa.

ejaculatory duct: canal passing sperm from vasa deferentia to exterior during sexual union; often modified to include seminal vesicle, prostate and intromittent organ.

eyes: small dark spots arranged in groups, as: *cerebral* eyes, when lying over or alongside cerebral organ; *frontal* eyes, when strewn over cephalic region of body; *marginal* eyes, when occurring along body margins; *submarginal* eyes in a row well separated from body margin; *tentacular* eyes lying in or around tentacles, or where tentacles would be, if present.

female antrum (vagina externa): distal region of vagina opening to exterior.

female copulatory complex: includes Lang's vesicle, if present, vagina externa, vagina media and vagina interna.

genital pores: openings of male and female copulatory complexes to exterior.

genito-intestinal canal: canal connecting vagina with intestinal trunk.

independent prostate: vesicular appendage of ejaculatory duct not conveying sperm.

interpolated prostate: modified part of ejaculatory duct, variously developed through which sperm pass during sexual union.

intestinal trunk: central tube in median line with lateral branches ramifying to body-margins.

intromittent organ: see penis-papilla and cirrus.

Lang's vesicle: variously developed blind terminus of vagina interna.

male antrum (antrum masculinum): space between male genital pore and intromittent organ.

male copulatory complex: consists of seminal vesicle, prostate and intromittent organ.

mouth: ventral, opens into pharyngeal chamber containing pharynx.

penis-papilla: muscular cone at end of male system projecting from roof of male antrum.

penis-pocket: inner chamber of male antrum enclosing penis-papilla.

penis-sheath: conical projection separating inner and outer chambers of male antrum.

pharynx: ruffled, bell-shaped or tubular fold of muscular tissue lying in pharyngeal chamber.

pharyngeal chamber or buccal cavity: contains pharynx.

prostate: (independent).

prostate: (interpolated).

prostatoid: pyriform musculo-glandular organ lying in parenchyma and opening into male antrum or on ventral surface of body.

seminal vesicle: muscular organ storing sperm.

'shell'-chamber (*vagina media*): part of vagina receiving secretion from investing 'shell'-glands.

spermiducal bulb or vesicle: distal part of vas deferens swollen and muscular.

tentacles: dorsal projections on body surface in cerebral region (nuchal tentacles) or folds of anterior margin of body (marginal tentacles).

uterine canals: two tubes lying alongside pharynx and receive eggs from oviducts.

vagina bulbosa: highly muscular female antrum.

vagina externa = female antrum.

vagina interna = proximal part of vagina into which uterine canals open.
vagina media = 'shell'-chamber.
vasa deferentia: sperm-canals linking vasa efferentia and ejaculatory duct.

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Ten new taxa of chiropteran myobiids of the genus *Pteracarus* (Acarina: Myobiidae)*

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INTRODUCTION

The myobiid genus *Pteracarus* Jameson & Chow was erected for *Myobia chalinolobus* Womersley (the type species), *Myobia pipistrellia* Radford, *Myobia minuta* Radford and *Pteracarus tenax* Jameson & Chow (Jameson & Chow, 1952). Then, Dusbábek (1973) presented a precise definition and detailed morphology for the genus, together with the descriptions of 14 species and some subspecies within three named and seven unnamed taxa as well as keys to both sexes of all known species. Since the genus *Pteracarus* has proved to be associated with the bat families Vespertilionidae (one of the largest families), Miniopteridae and Thyropteridae, a large number of species of the genus are expected to occur in both the Old and New Worlds.

The present paper deals with the description of 10 new taxa. The nomenclature of dorsal setae on the idiosoma is basically the same as in Dusbábek (1973), although his female genital setae *pg*, g_1, g_2 and anal setae a_3 are regarded, in the present paper, as g_1, g_3, g_4 and g_7, respectively. Accordingly, the female genital and anal setae are thought to comprise $g_{1,3\text{-}7}$, exclusive of g_2, and *ae* and *ae*. Moreover, setae on the idiosomal venter are named following Fain (1973*a*). Numbers of setae and solenidia on tarsus I are five and four, respectively, instead of six and three as in Dusbábek (1973).

All the specimens recorded below were taken from bats deposited in the collections of the leading museums in Europe and the United States, and data for every specimen follows labels on its host in the respective museums. The abbreviations for the museums are as follows: BMNH—British Museum (Natural History), London; SMF—Forschungs-Institut Senckenberg, Frankfurt; MNHN—Muséum National d'Histoire Naturelle, Paris; AMNH—American Museum of Natural History, New York; USNM—U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C; FMNH—Field Museum of Natural History, Chicago.

Measurements given in the text are in μm.

DESCRIPTIONS OF NEW MITES

I. Mites with a dorsal seta on genu IV (a total of 6 setae); *d*-series of setae complete (d_1–d_5) (Dusbábek, 1973), or d_4 and d_5 present in the female.

Pteracarus hesperoptenis sp. nov.

FEMALE (Figs 1 & 2). Gnathosoma broad, wider than long. Idiosoma stout. Setae *vi* longer than *sc i*, barbed and fine distally; *ve, sc e* and l_1 very long; d_1–d_5 well developed; distance between d_1 and d_2 greater than between succeeding ones; d_5 situated on posterior-level of legs IV; ic_1 and 2 *cx* I minute; ic_2 and *cx* II_1 on sclerites; ic_4 and *cx* IV spiniform, on a sclerite; g_1 inferior in size to ic_4 and *cx* IV; g_3 and g_4 thinner than g_1; spermatheca not visible. Legs stout; leg I short and thick, with terminal claws; second claw on legs II–IV slightly smaller than first one; antero-lateral seta on trochanter, femur and genu of leg I spiniform. Chaetotaxy of gnathosoma, idiosoma and legs as in Figs 1 and 2; tarsus I with five setae and four solenidia, but setations on other segments as in Dusbábek (1973); dorsal setae on femur I and tibia IV long.

MEASUREMENTS. Body (= gnathosoma + idiosoma) 400 long, 245 wide; *vi* 20; *ve* 93; *sc i* 10; *sc e* 195; d_1, d_2, d_3, d_4 and d_5 33, 32, 38, 38 and 47, respectively; l_1 *ca.* 180; l_3 18; l_4 13; ic_4 22; *cx* IV 20.

MATERIAL EXAMINED. Holotype female ex *Hesperoptenus tomesi*, Malaya, date uncertain, in the collection of BMNH (Host accession Nos BM 74.455–6).

The holotype is deposited in the collection of the BMNH (BM 1987.9.9.1).

DIAGNOSIS. *Pteracarus hesperoptenis* sp. nov. is defined from a single female specimen on the basis of well-developed $d_{1\text{-}5}$ situated anterior to the posterolateral margin of legs IV and ventral sclerite bearing ic_4 and *cx* IV, characters not found in the other species. It is often difficult to identify an unknown sex when a species is described on the opposite sex, but the partner male of *P. hesperoptenis* should be easily recognized by the unique sclerite bearing ic_4 and *cx* IV.

Pteracarus rhogeesis sp. nov.

MALE (Figs 3 & 4). Gnathosoma wider than long dorsally. Setae *vi* and *sc i* minute; *ve, sc e* and l_1 relatively short especially posterior to barb and ending abruptly; d_1 and d_2 conspicuous, probably apart from genital shield. Genital shield probably small; four pairs of genital setae visible; postero-median (= gm_1 in Dusbábek, 1973) thick and swollen apically; enis long. Ventral setae ic_4 and *cx* IV spiniform. Leg I with a pair of terminal claws; paired claws on legs II–IV subequal in size to each other; leg setae as in Figs 3 and 4.

MEASUREMENTS. Body 310 long by 200 wide; *vi* 3; *ve* 65; *sc i* 3; *sc e* 80; l_1 83; l_3 14; d_1 13; d_2 15; ic_4 15; *cx* IV 13; penis *ca.* 200.

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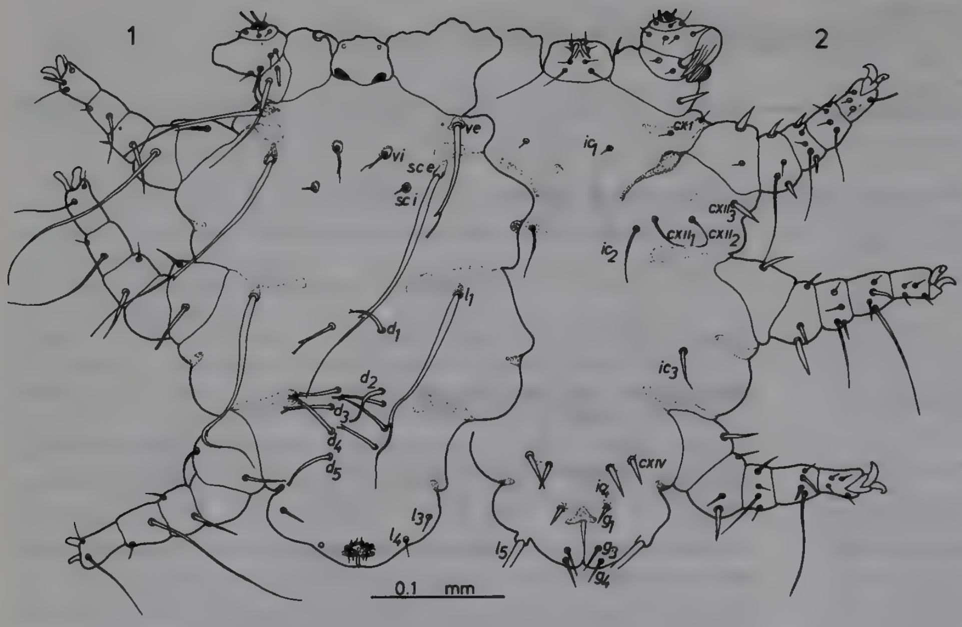
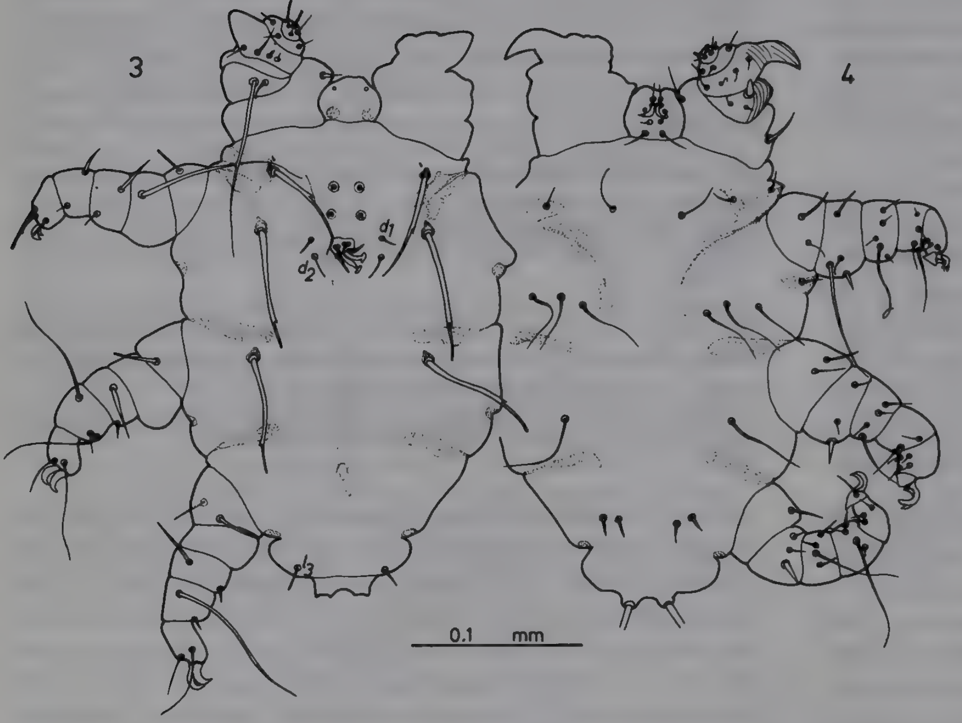
* Supported financially by Overseas Scientific Research Grant Nos 57041019 and 5803013 from the Ministry of Education, Science and Culture, Japan. Contribution No. Ac–15.



Figs 1–2 *Pteracarus hesperoptenis* sp. nov.: **female** dorsum (1); venter (2).



Figs 3–4 *Pteracarus rhogeesis* sp. nov.: **male** dorsum (3); venter (4).

FEMALE (Figs 5 & 6). Gnathosoma as long as wide. Setae *vi* minute, longer than *sc i*; *ve, sc e* and l_1 short; d_1–d_3 vestigial; d_4 and d_5 short but conspicuous; l_3 thicker and longer than l_4. Ventral setae, legs and leg setae as in male (Figs 5 & 6). Spermatheca as in Fig. 5.

MEASUREMENTS. Body 400 (allotype) (370–400, 4 paratypes) long by 225(225–235) wide; *vi* 12(10–13); *ve* 85(78–88); *sc i* 8(5–7); *sc e* 88(85–93); d_4 13(12–15); d_5 13(14–17); l_1 78(75–83); l_3 25(23–28); l_4 15(15–22); ic_4 15(17–18); *cx* IV 16(15–17).

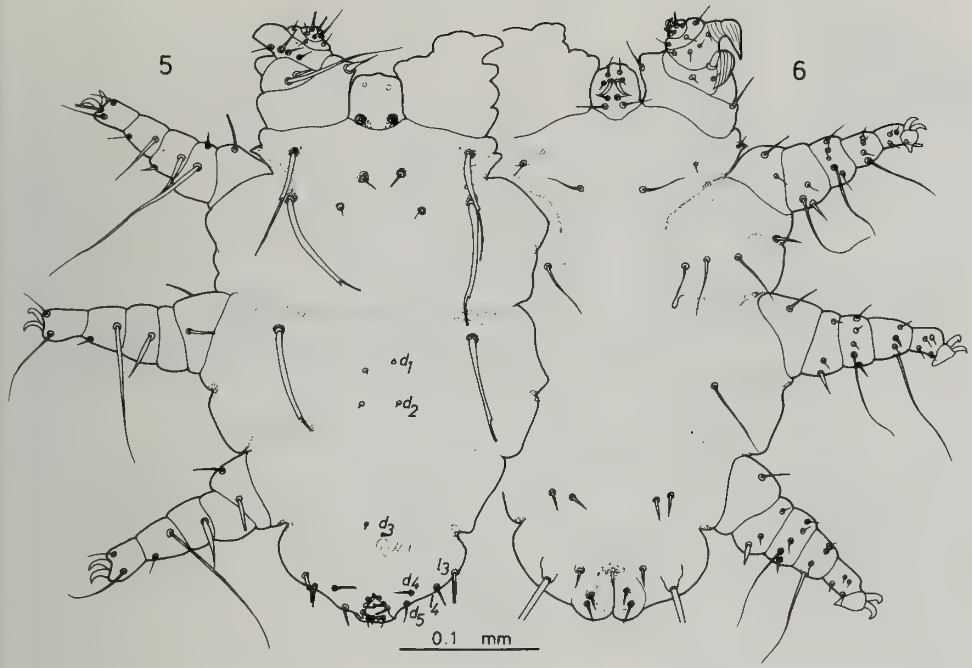
MATERIAL EXAMINED. Holotype male, allotype female and four paratype females ex *Rhogeesa tumida*, Avellana, Sta. Rosai, Guatemala, IV–1974 (AMNH 243952–5).

The holotype, allotype and a paratype are deposited in the collection of the Department of Entomology, AMNH, and two and one paratypes are in the collections of the BMNH (BM 1987.9.9.2–3) and the author, respectively.

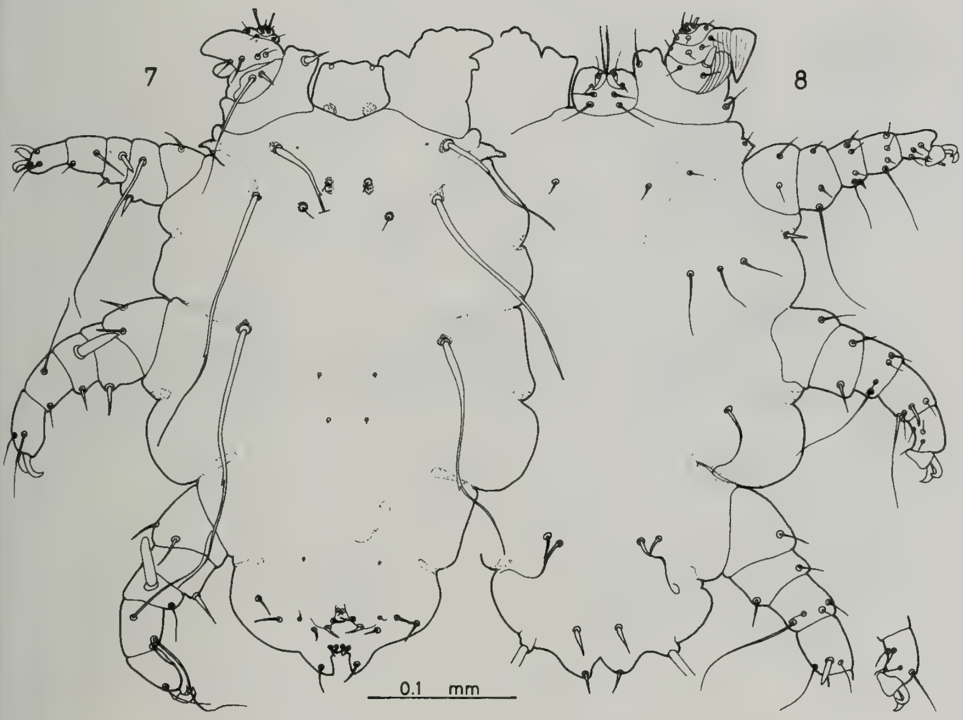
DIAGNOSIS. *Pteracarus rhogeesis* sp. nov. is characterized by the male genital shield bearing unique posteromedian setae that are boot-like and by short dorsal setae *ve, sc e* and l_1 in both sexes.

Pteracarus genualis sp. nov.

FEMALE (Figs 7 & 8). Gnathosoma pentagonal. Seta *vi* slightly thicker and shorter than *sc i*; *ve, sc e* and l_1 long; d_1–d_3 vestigial; d_4 inferior in size to d_5; *cx* II_3, spiniform; ic_4



Figs 5–6 *Pteracarus rhogeesis* sp. nov.: **female** dorsum (5); venter (6).



Figs 7–8 *Pteracarus genualis* sp. nov.: **female** dorsum (7); venter (8).

setiform and long; *cx* IV spiniform. Leg I broad and rather short, lacking terminal claws; dorsal seta on genua II–IV spiniform and not striated. Male unknown.

MEASUREMENTS. Body 420 long by 270 wide. Setae *vi* 11; *ve* 115; *sc i* 15; *sc e* 185; l_1 *ca*. 170; l_3 16; l_4 16; ic_4 more than 50; spines on genua II–IV 21 long by 5 wide, 35 × 9 and 33 × 8, respectively.

MATERIAL EXAMINED. Holotype female ex *Ia io*, Kiang-Si, China, date uncertain (BM 2512.6.2).

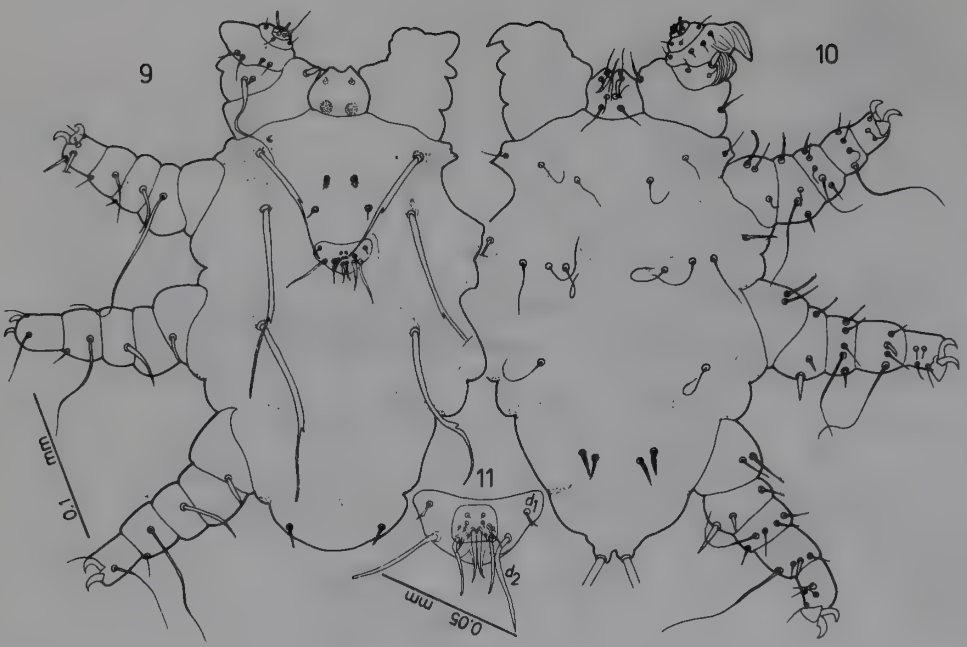
The holotype is deposited in the collection of the BMNH (BM 1987.9.9.4).

DIAGNOSIS. *Pteracarus genualis* sp. nov. is characterized by the thickened and spiniform dorsal seta on genua II–IV, a character that has not been found in other species. The paired setae ventrally in coxal region IV, ic_4 and *cx* IV, are different from each other in the present new species. Such a pair of setae is found only in *Pteracarus completus vrazi* Dusbábek and Wilson (Dusbábek, 1973).

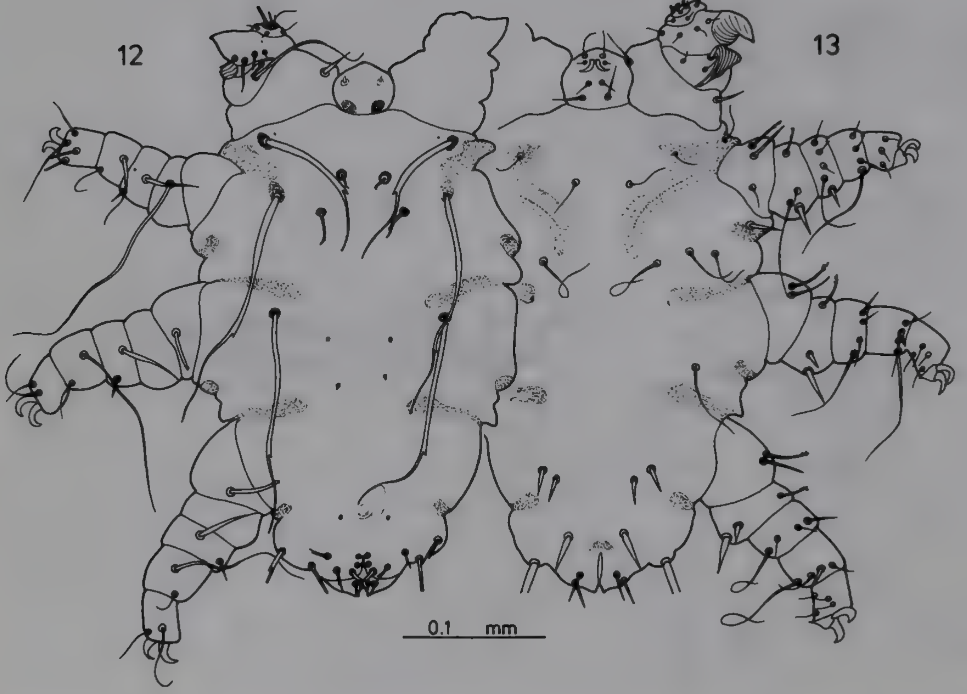
The specific name *genualis* is adopted in contrast with *tibialis* that indicates tibiae III and IV each bearing a stout, lanceolate and striated dorsal seta in the female.

Pteracarus histotis sp. nov.

MALE (Figs 9, 10 & 11). Gnathosoma shorter than wide dorsally. Setae *vi* inferior in size to *sc i*; *ve, sc e* and l_1 long; d_2 long. Genital shield distinctly posterior to basal level of *sc e*,



Figs 9–11 *Pteracarus histotis* sp. nov.: **male** dorsum (9); venter (10); genital shield (11).



Figs 12–13 *Pteracarus histotis* sp. nov.: **female** dorsum (12); venter (13).

bearing four pairs of minute setae, a pair of moderate setae, two pairs of long setae and barbed d_1; penis long. Ventral setae of coxal regions I–III fine and long; ic_4 and *cx* IV spiniform and striated; ic_4 slightly thinner than *cx* IV. Leg I with terminal claws; antero-lateral seta on coxae II–IV and femora II–IV weakly barbed; the two ventral setae on femora III and IV setiform.

Measurements. Body 320 long by 190 wide; *vi* 4; *ve* 78; *sc i* 6; *sc e* 125; l_1 120; l_3 13; d_1 6; d_2 35; longest genital seta 21; penis *ca*. 195; ic_4 15; *cx* IV 18.

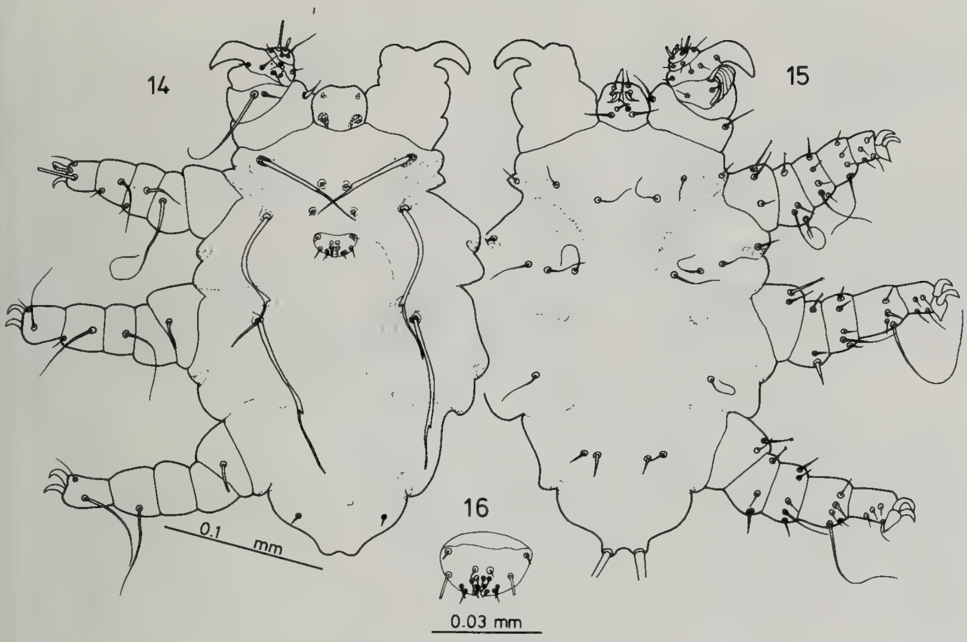
Female (Figs 12 & 13). Setae *vi* distinctly shorter than *sc i*; *ve*, *sc e* and l_1 long; d_1–d_3 vestigial; d_4 conspicuous, slightly shorter than d_5; l_3 shorter than l_4; ic_4 and *cx* IV subequal in size. Spermatheca as in Fig. 12. Other characters as in the male.

Measurements. Body 380 long by 220 wide; *vi* 12; *ve ca*. 110; *sc i* 26; *sc e ca*. 175; d_4 11; d_5 15; l_1 *ca*. 165; l_3 23; l_4 25; ic_4 20; *cx* IV 23.

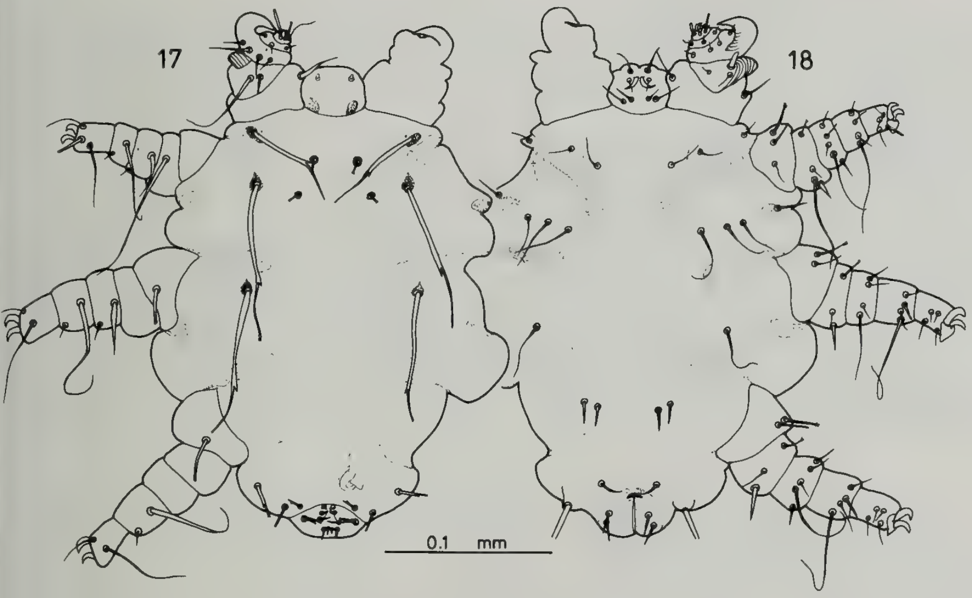
Material examined. Holotype male and allotype female ex *Histiotus macrotus*, Jujuj, Argentina, date uncertain (USNM 10105).

The types are deposited in the collection of the USNM.

Diagnosis. *Pteracarus histotis* sp. nov. shares more characters with *Pteracarus aculeus* Dusbábek & Lukoschus than with any other member of the genus. However, both species are



Figs 14–16 *Pteracarus pizonychos* sp. nov.: **male** dorsum (14); venter (15); genital shield (16).



Figs 17–18 *Pteracarus pizonychos* sp. nov.: **female** dorsum (17); venter (18).

easily distinguished from each other by differences in the genital shield and setae on it in the male. The number of genital setae is more, the longest genital setae are longer and d_2 is much longer in *P. histotis* than in *P. aculeus*. In the female, setae *vi* are distinctly shorter than *sc i* in *P. histotis*, while these setae are subequal in length in *P. aculeus*.

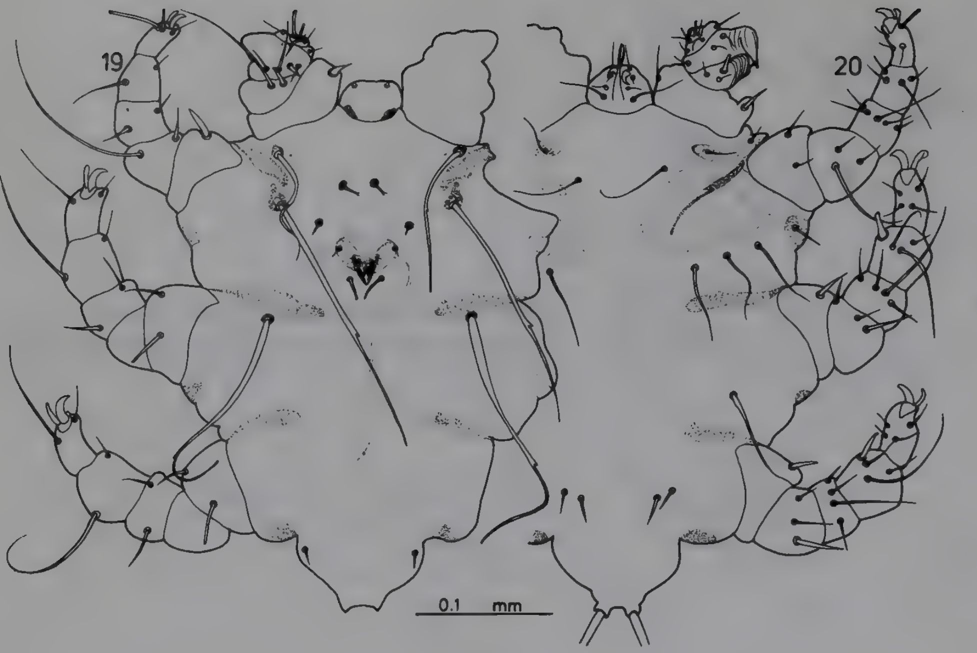
II. Mites without dorsal seta on genu IV (a total of five setae) (Dusbábek, 1973), and with d_4 and d_5 in the female.

Pteracarus pizonychos sp. nov.

MALE (Figs 14, 15 & 16). Gnathosoma almost as long as wide. Setae *vi* minute; *sc i* more conspicuous than *vi*, situated on asal level of *sc e*; *ve, sc e,* l_1 long and similar to one another; l_3 weak; ventral setae not so strong; ic_4 and *cx* IV setiform. Genital shield situated distinctly posterior to basal level of *sc e*, bearing seven pairs of genital setae; d_1 much shorter than postero-median genital seta; penis long and rather thin. Leg I with a pair of terminal claws; paired claws on legs II–IV subequal in size to each other; antero-lateral seta on coxae II–IV and femora II–IV barbed apically.

MEASUREMENTS. Body 290 (holotype)–280 (paratype) long by 175–165 wide; *vi* 3–3; *ve* 68–67; *sc i* 4–5; *sc e ca.* 85–93; l_1 95–93; l_3 6–6; d_1 3–3; d_2 6–8; penis *ca.* 175–*ca.* 170; ic_4 11–10; *cx* IV 8–8.

FEMALE (Figs 17 & 18). Idiosoma rounded. Setae *vi* and *sc i*



Figs 19–20 *Pteracarus pipistrellius maximis* ssp. nov.: **male** dorsum (19); venter (20).

subequal; d_1–d_3 lacking on allotype and 2 paratypes but only d_3 discernible on the third paratype; d_4 well developed, inferior in length to d_5; l_3 distinctly longer than l_4. Spermatheca as in Fig. 17. Other characters as in the male.

MEASUREMENTS. Body 360 (allotype) (360–390, 3 paratypes) long by 270(260–280) wide; *vi* 9(8–10); *ve* 82(83–91); *sc i* 8(7–8); *sc e* 115(128–140); l_1 112(120–125); l_3 28(30–34); l_4 24(20–23); d_4 14(13–13); d_5 15(17–20); ic_4 15(15–17); *cx* IV 14(13–13).

MATERIAL EXAMINED. Holotype male, allotype female, a paratype male and three paratype females ex *Pizonyx vivesi*, Partida Is., Lower California, U.S.A., 9–III–1936 (USNM 260575–80).

The holotype, allotype and a paratype female are deposited in the USNM collection; a paratype female is in the collection of the BMNH (BM 1987.9.9.5); and a pair of male and female paratypes are in the collection of the author.

DIAGNOSIS. *Pteracarus pizonychos* sp. nov. is allied to *Pteracarus minutus* sspp. in having the same type of male genital shield. However, the genital shield is situated more posteriorly and bears distinctly shorter d_1 in the new species than in *P. minutus* sspp. Measurements for both sexes are larger in *pizonychos* than in *P. minutus* sspp. Moreover, the barbed antero-lateral seta on coxae and femora II–IV of *P. pizonychos* is not found in *P. minutus* sspp.

Females of all the preceding species bear d_1–d_5 dorsally on the idiosoma. In *P. pizonychos*, setae d_1–d_3 are lacking, while d_4 and d_5 are well developed. However, setae d_3 are discernible exceptionally on a single paratype, suggesting that the regression of d_1–d_3 is incomplete and that mites with only d_4 and d_5 are not so far from those with d_1–d_5 phylogenetically. Accordingly, the presence of d_4 and d_5 seems to have the same meaning as the *d* series of setae being complete.

The six species, *P. compactus* Fain, *P. faini* Uchikawa, *P. miniopteri* Uchikawa, *P. minutus* sspp., *P. peruvianus* Fain and *P. tibialis* Dusbábek, and *P. pizonychos* belong to the group with five setae on genu IV. All these species lack d_1–d_3 and bear d_4 and d_5. It is reasonable to presume that dorsal setae on genu IV and d_1–d_3 have disappeared from the type with six setae on genu IV and d_1–d_5 on the idiosomal dorsum.

III. Mites with a dorsal seta on genu IV (a total of six setae); *d* series lacking d_5 in the female (Dusbábek, 1973).

Pteracarus pipistrellius maximis ssp. nov.

MALE (Figs 19 & 20). Gnathosoma shorter than wide. Setae *vi* superior in size to *sc i*; *sc i* situated posterior to bases of *sc e*; *ve*, *sc e* and l_1 long; l_3 minute; ventral setae ic_4 and *cx* IV spiniform. Genital shield bearing two pairs of minute setae, two pairs of modified postero-median setae and d_1; d_2 off the shield; penis curved distally. Leg I with a pair of terminal claws; paired claws on legs II–IV unequal in size to each other.

MEASUREMENTS. Body 390 long by 250 wide; *vi* 11; *ve ca.* 103; *sc i* 10; *sc e* 205; l_1 *ca.* 190; l_3 12; d_1 8; d_2 22; penis *ca.* 168.

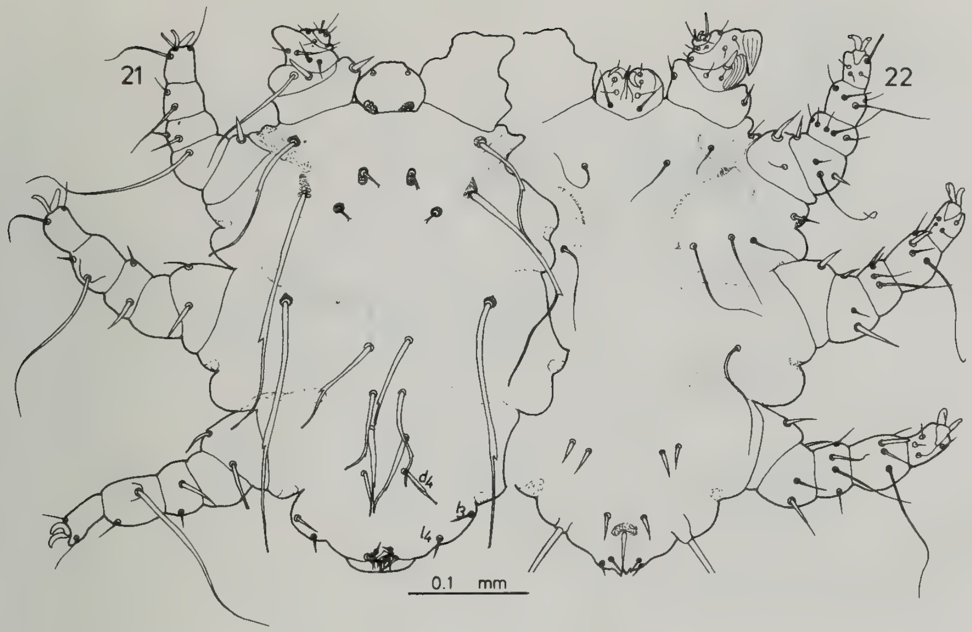
FEMALE (Figs 21 & 22). Dorsal setae d_1–d_4 long; d_4 situated almost on posterior level of leg IV. Other characters as in male.

MEASUREMENTS. Body 430 (allotype) (420–430, two paratypes) long by 290(290–290) wide; *vi* 15(13–15); *ve ca.* 125(120–120); *sc i* 13(10–13); *sc e* 210(228–208); d_1 92(90–95); d_2 75 (73–85); d_3 73(67–73); d_4 40(45–41); l_1 205(210–208); l_3 15(15–15); l_4 17(16–18); ic_4 23(23–23); *cx* IV 18(20–18).

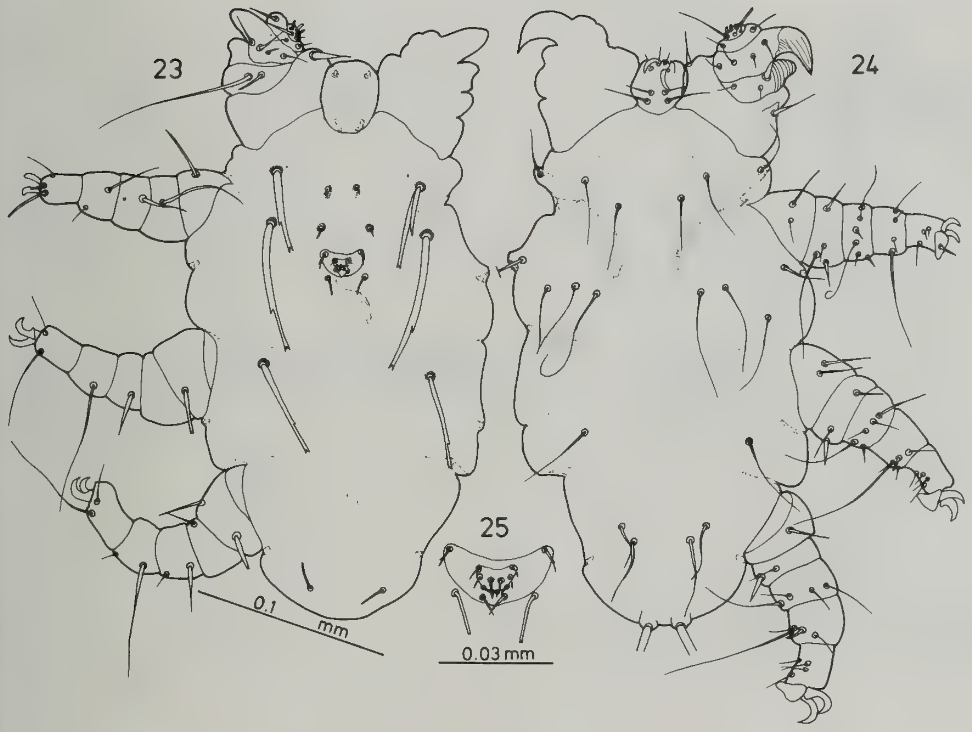
MATERIAL EXAMINED. Holotype male, allotype female and a paratype female ex *Nyctalus maximus*, Pisa, Italy, date uncertain (USNM 86623–4); a paratype female ex *Nyctalus lasiopterus*, Creuse, France, date uncertain.

The holotype and allotype are deposited in the USNM collection; a paratype female is in the collection of MNHN; and a paratype female is in the collection of the author.

DIAGNOSIS. Those mites with the male genital shield as described above and with setae d_1–d_4 in the female long and



Figs 21–22 *Pteracarus pipistrellius maximis* ssp. nov.: **female** dorsum (21); venter (22).



Figs 23–25 *Pteracarus mimetillius* sp. nov.: **male** dorsum (23); venter (24); genital shield (25).

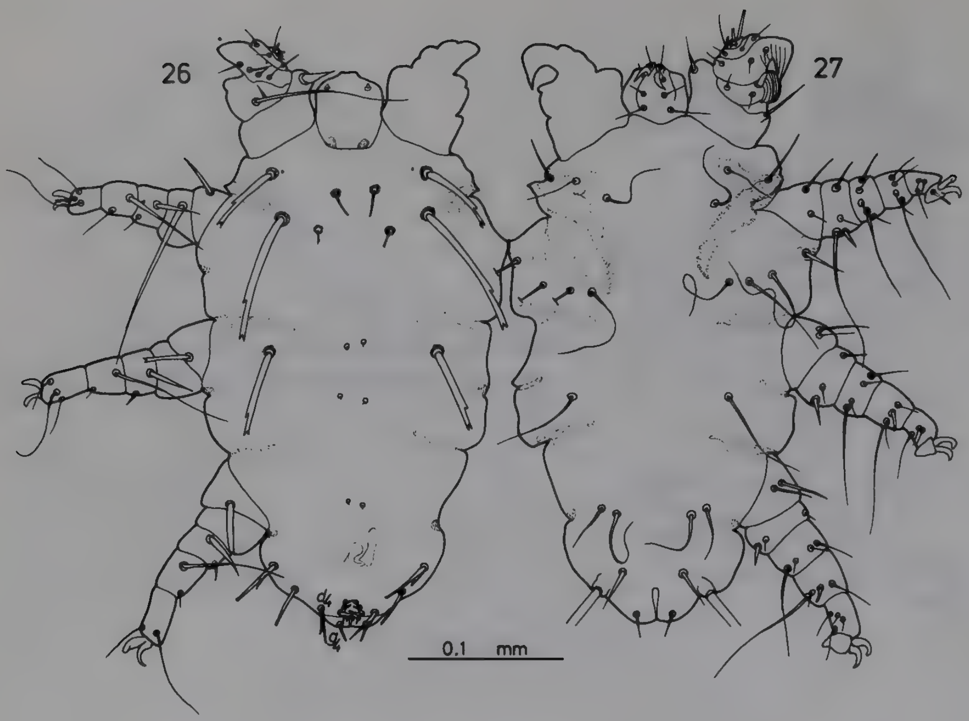
arranged unusually within the region of legs IV are regarded as subspecies of *Pteracarus pipistrellius* (Radford) (Dusbábek, 1973). The nominate subspecies and subspecies *tenax* Jameson & Chow have been proposed on the basis of setal lengths. *Pteracarus pipistrellius maximus* ssp. nov. is differentiated from those two subspecies by its larger measurements for the body, *ve, sc e* and l_1 of both sexes and for d_1, d_2 and d_3 of the female. Dorsal seta *sc i* is situated posterior to the basal level of *sc e* in the male of the present subspecies, while the corresponding seta is on the basal level of *sc e* in both the nominate subspecies and *tenax*.

The hosts of *P. pipistrellius maximis* from Italy and France were differently named in the collections of the two museums as recorded above, but it is highly probable that they are conspecific.

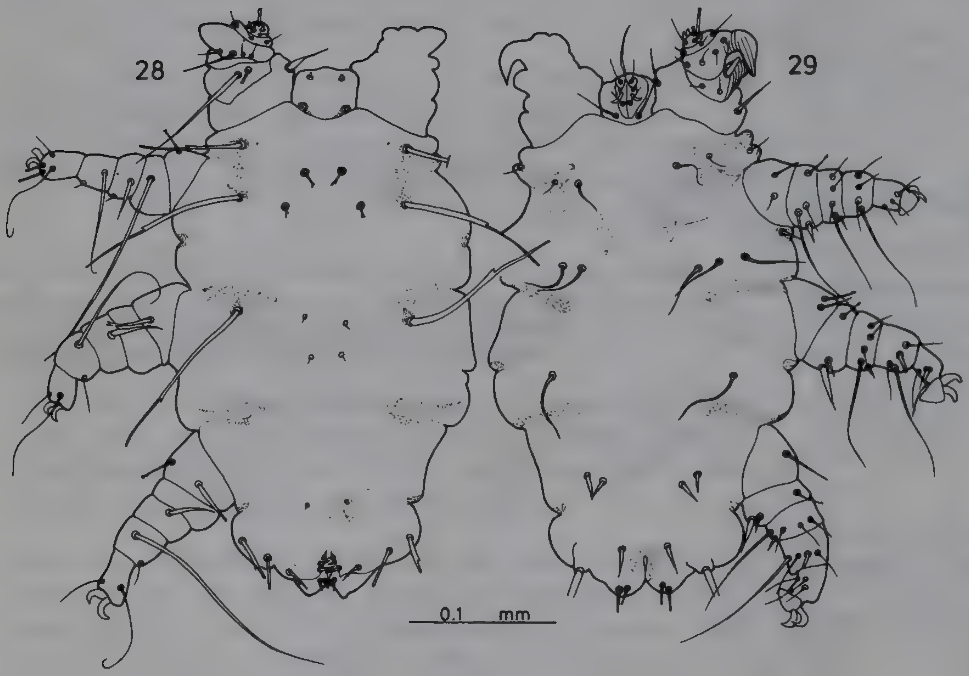
Pteracarus mimetillius sp. nov.

MALE (Figs 23, 24 & 25). Gnathosoma longer than wide. Setae *vi* minute, inferior in size to *sc i*, d_1 or d_2; *sc i* situated almost on basal level of *sc e*; *ve, sc e* and l_1 thick and relatively short, barbed and apically bifurcated; all ventral setae, inclusive of ic_4, *cx* IV and *cx* II 3, setiform, fine and long. Genital shield bearing six pairs of genital setae and d_1; d_2 off shield; penis long. All legs stout; leg I with a pair of terminal claws; paired claws on legs II–IV subequal in size to each other.

MEASUREMENTS. Body 285 (holotype)–260 (paratype) long by 150–150 wide; *vi* 3–4; *ve* 47–48; *sc i* 5–5; *sc e* 71–80; l_1 50–53; l_3 18–18; d_1 8–8; d_2 14–15; penis *ca.* 155–*ca.* 140.



Figs 26–27 *Pteracarus mimetillius* sp. nov.: **female** dorsum (26); venter (27);.



Figs 28–29 *Pteracarus nycticeius* sp. nov.: **female** dorsum (28); venter (29).

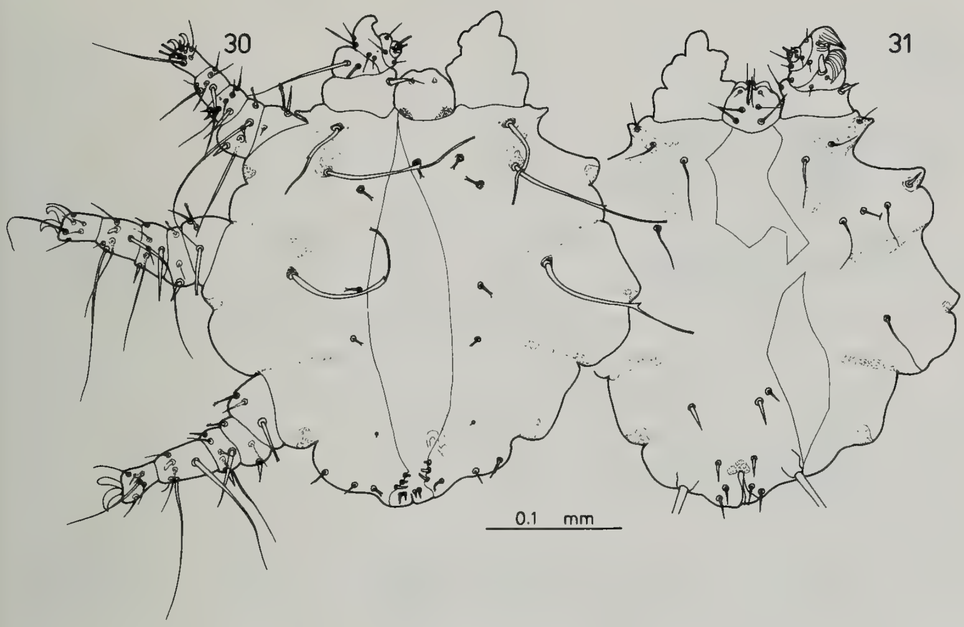
FEMALE (Figs 26 & 27). Setae *vi* distinctly longer than *sc i*; d_1–d_3 vestigial; d_4, l_3 and l_4 well developed. Spermatheca as in Fig. 26. Other characters as in the male.

MEASUREMENTS. Body 365 (allotype) (360–380, four paratypes) long by 200(190–210) wide; *vi* 20(15–19); *ve* 54(55–60); *sc i* 12(9–12); *sc e* 92(88–98); d_4 28(25–28); l_1 63(63–70); l_3 35(30–35); l_4 29(30–41).

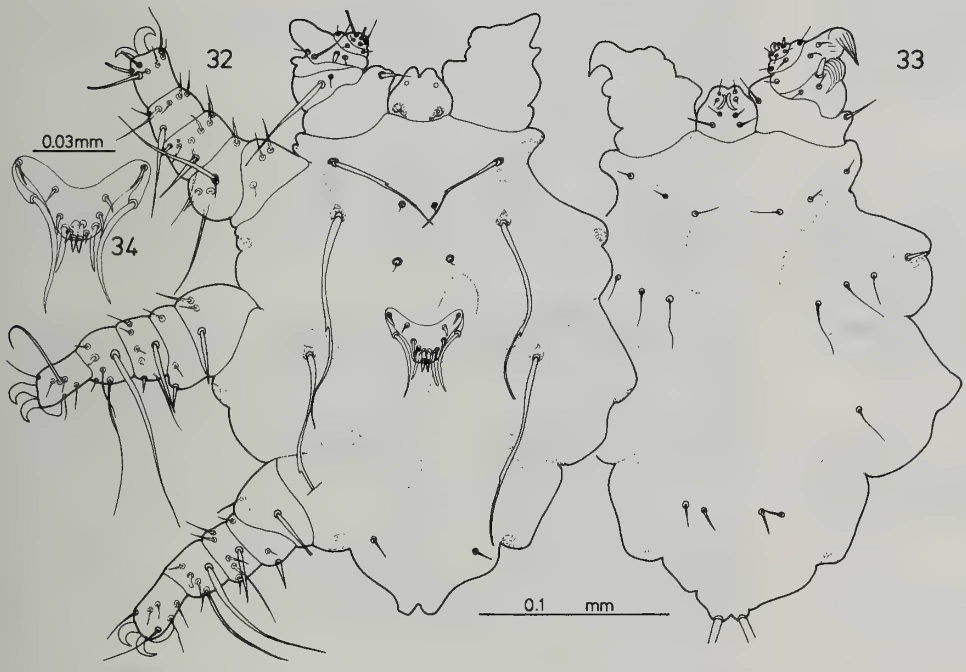
MATERIAL EXAMINED. Holotype male, allotype female and three paratype females ex *Mimetillus moloneyi*, La Maboki, Republic of Central Africa, 1965, in the collection of MNHN; a male paratype ex *M. moloneyi*, Bo, Sierra Leone, date uncertain (BM 60.304–6); and a female paratype ex *M. moloneyi*, date uncertain (BM 64.1786–8).

The holotype and allotype are deposited in the collection of the MNHN; a pair of male and female paratypes is in the collection of the BMNH (BM 1987.9.9.6–7); and three paratype females are in the collection of the author.

DIAGNOSIS. Among the known species of the genus *Pteracarus*, *P. charinolobus* (Womersley), *P. microdorsalis* Fain & Lukoschus and the preceding species, *P. pipistrellius* (Radford), are characterized by lacking d_5 dorsally on the female idiosoma. *Pteracarus mimetillius* sp. nov. is easily differentiated from the above three species by its unique setae on the idiosomal venter. Thick, relatively short and apically bifurcated setae *ve, sc e* and l_1 of both sexes are also characteristic of the new species.



Figs 30–31 *Pteracarus brevis* sp. nov.: **female** dorsum (30); venter (31).



Figs 32–34 *Pteracarus tylonycteris* sp. nov.: **male** dorsum (32); venter (33); genital shield (34).

Pteracarus nycticeius sp. nov.

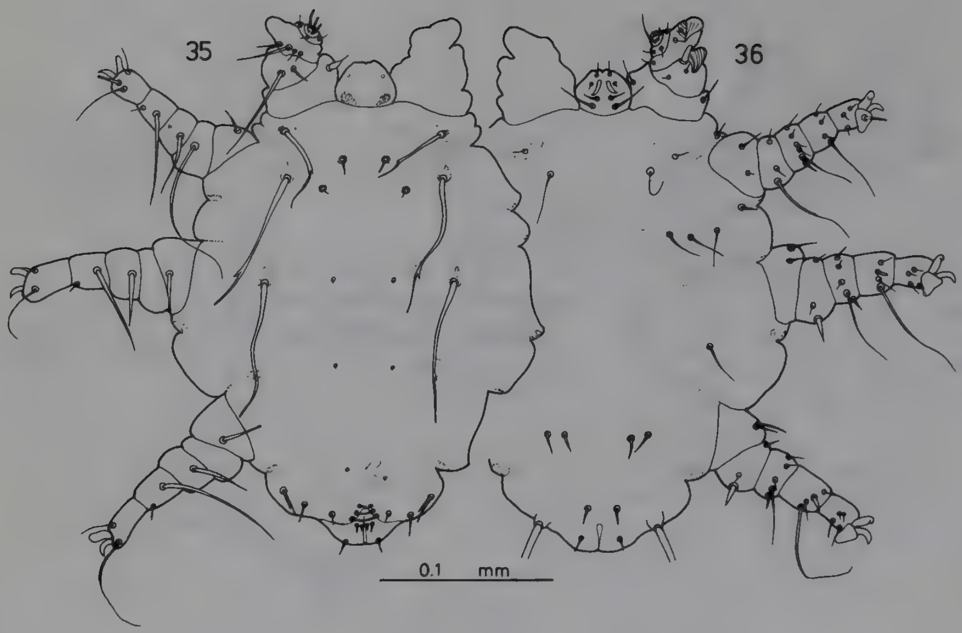
Female (Figs 28 & 29). Gnathosoma wider than long. Setae *vi* superior in size to *sc i*; *sc i* almost on basal level of *sc e*; *ve*, *sc e* and l_1 relatively short and rather slender; d_1–d_3 minute; d_4 well developed but distinctly shorter than l_3 and l_4; ventral setae ic_4 and *cx* IV spiniform. Spermatheca as in Fig. 28. Leg I with a pair of claws; paired claws on legs II–IV subequal in size to each other; spines ventrally on femora II–IV 1, 2 and 2, respectively; antero-lacteral seta on coxae II–IV and femora II–IV weakly barbed apically. Male unknown.

Measurements. Body 365 (holotype) (355–420, four paratypes) long by 205(220–240) wide; *vi* 12(10–10); *ve* 75(78–83); *sc i* 10(8–10); *sc e* 120(112–123); d_4 17(14–17); l_1 120 (115–130); l_3 33(28–28); l_4 28(22–25); ic_4 17(18–20); *cx* IV 17(16–18).

Material examined. Holotype female and four paratype females ex *Nycticeius schliefferi*, Boutilimit, Pays Trarza, Sahara, Mauritanie, date uncertain, in the collection of MNHN.

The holotype and a paratype are deposited in the collection of MNHN and 1 and 2 paratypes are in the collections of the BMNH (BM 1987.9.9.8) and the author, respectively.

Diagnosis. *Pteracarus nycteceius* sp. nov. resembles *P. microdorsalis* among the mites belonging to a group lacking dorsal seta d_5. The new species is distinct in having two spines ventrally on femora III and IV instead of one each on those segments as in *P. microdorsalis*.



Figs 35–36 *Pteracarus tylonycteris* sp. nov.: **male** dorsum (35); venter (36).

Since two ventral spines on femora III and IV are found only in *P. aculeus* Dusbábek & Lukoschus, parasitic on *Eptesicus* spp., and *P. histotis*, both of which are known from both sexes, the partner male of *P. nycteceius* may be easily identified on the basis of this character and host record.

Pteracarus brevis sp. nov.

Female (Figs 30 & 31). Gnathosoma wider than long. Idiosoma as long as wide; *vi* and *sc i* short yet conspicuous; *ve, sc e* and l_1 long; d_1 and d_2 conspicuous; d_3 minute; d_4, l_3 and l_4 conspicuous but short; ic_4 and *cx* IV spiniform. Spermatheca as in Fig. 30. Leg I with a pair of terminal claws; antero-lateral seta on trochanters II–IV and femora II–IV barbed.

Measurements. Body *ca.* 330 long; *vi* 12; *ve* 65; *sc i* 12; *sc e* *ca.* 120; d_1 8; d_2 6; d_4 8; l_1 *ca.* 125; l_3 15; l_4 15; ic_4 18; *cx* IV 13.

Material examined. Holotype female (damaged) ex *Philetor brachypterus verascundus*, Kempas, Paloh, Klang, Johore, Malaya, 8–V–1970 (AM 247518–25).

The holotype is deposited in the collection of the Department of Entomology, AMNH.

Diagnosis. *Pteracarus brevis* sp. nov. is distinct in having the idiosoma as long as wide, a feature that is lacking in all other known species of the genus *Pteracarus*.

Pteracarus tylonycteris sp. nov.

Male (Figs 32, 33 & 34). Gnathosoma wider than long. Setae *vi* just anterior to basal level of *sc e*, minute; *sc i* distinctly posterior to basal level of *sc e*; *ve, sc e* and l_1 long; ventral setae ic_4 and *cx* IV spiniform. Genital shield closer to basal level of l_1 than to that of *sc e*; bearing six pairs of genital setae, d_1 and d_2; d_2 relatively long; penis sinuate. Leg I with a pair of terminal claws; paired claws on legs II–IV unequal in size to each other.

Measurements. Body 290 long by 210 wide; *vi* 3; *ve* 60; *sc i* 4; *sc e* *ca.* 110; l_1 108; l_3 11; d_1 8; d_2 45; ic_4 13; *cx* IV 13; penis *ca.* 160.

Female (Figs 35 & 36). Setae *vi* slightly longer than *sc i*; *vi* distinctly anterior to basal level of *sc e*; *sc i* slightly posterior to basal level of *sc e*; d_1–d_3 vestigial d_4 conspicuous but much inferior in size to l_3 and l_4; l_3 and l_4 relatively short. Spermatheca as in Fig. 35. Other characters as in the male.

Measurements. Body 310 (allotype) (200–300, two specimens) long by 245(215–220) wide; *vi* 10(10–8); *ve* 65(60–55); *sc i* 7(8–7); *sc e* 110(110–98); d_4 8(7–6); l_1 108(115–92); l_3 18(23–18); l_4 18(22–15); ic_4 14(13–13); *cx* IV 10(10–12).

Material examined. Holotype male and allotype female ex *Tylonycteris pachypus*, Pertjut Medan, Sumatra, 1970 (SMF 39455–674); one female from the same host, Perak, Malaya, 24–I–1971 (AM 236207–11); one female from the same host, Ulu Langat Forest Reserves, Kajang, Selangor, Malaya (BM 60.1405–20); one female ex *Tylonycteris* sp. from Thailand as in Uchikawa & Kobayashi (1978).

All four specimens have been returned to the museums from which they were originally obtained, whilst the Thai specimen is in the collection of the author.

Diagnosis. Dusbábek (1973) described the male of a valid but anonymous species, *Pteracarus* sp. E, taken from *Tylonycteris robustula* in Malaysia. *Pteracarus tylonycteris* sp. nov. resembles his species, yet is differentiated from the latter by specific arrangement of genital setae on the male genital shield as well as longer *ve*. The nature of the extero-dorsal seta on femur I is also different in the two species.

Uchikawa and Kobayashi (1978) recorded a female of a *Pteracarus* species taken from *Thylonycteris* in Thailand. Although dorsal setae d_1–d_3 are lacking in the original figure (Uchikawa & Kobayashi, 1978, Fig. 16), these setae are discernible on that specimen, and measurements for all parts are within the ranges for the above allotype and two other females. Thus, their specimen is identifiable as the female of *P. tylonycteris*.

Table 1 Sorting of the 21 previously known and nine new species of the genus *Pteracarus* according to the chaetotaxy on genu IV and dorsally on female opisthosoma.

Dorsal seta on genu IV	d_1–d_3	d_5	Species
+	+	+	_aculeus, completus, robustus, submedianus, shealsi, macfarlanei, hesperoptenis_*, _rhogeeis_*, _genualis_*, _histotis_*
		−	_chalinolobus, pipistrellius, microdorsalis, breviatus_[‡], _mimetillius_*, _nycticeius_*, _brevis_*, _tylonycteris_*
	−	+	_elegans_
−	−	+	_compactus, dusbabeki, faini, miniopteri, minutus, mirabilis, pervianus, pusillus, tibialis_[†], _pizonychos_*

* New species.
† Based only on the female. *P. holubi* is known only from the male belonging to a group with a dorsal seta on genu IV.
‡ Setae d_5 of *P. breviatus* in the original description are g_4 in reality as shown in figs 5–6 in Fain & Aellen, 1979*b*.

DISCUSSION

Dusbábek (1973) reviewed 14 species of the genus *Pteracarus*, inclusive of two, three and two subspecies of *P. completus* Dusbábek and Wilson, *P. minutus* (Radford) and *P. pipistrellius* (Radford), respectively, and listed a further seven anonymous species (Spp. A–G). Of those named and unnamed species, *P. scutulatus* Fain and Coffee was synonymized with *P. pusillus* (Lawrence) (Fain, 1978*a*); *Pteracarus* sp. A was regarded as being conspecific with *P. chalinolobus* (Womersley) (Fain & Lukoschus, 1979); and *Pteracarus* sp. F was named *P. dusbabeki* by Uchikawa *et al.* (1980). Morphologically, the male and female of *P. tibialis* Dusbábek were shown to have different chaetotaxies on leg IV. Since both sexes usually share the same leg chaetotaxy, it is necessary to re-examine the males from the type host. In this connection, the males recorded by Dusbábek (1973) had been taken not from the type host, *Myotis myotis* (Dusbábek, 1970), but from *Nyctalus noctula*.

The species or subspecies that have been added to the above are as follows: *P. shealsi* Fain, 1973*b*; *P. macfarlanei* Fain, 1973*b*; *P. peruvianus* Fain, 1978*b*; *P. faini* Uchikawa, 1978*a*; *P. pusillus thailandensis* Uchikawa & Kobayashi, 1978; *Pteracarus* sp. (female) Uchikawa & Kobayashi, 1978 (=*P. tylonycteris* sp. nov.); *P. miniopteri* Uchikawa, 1978*b*; *P. microdorsalis* Fain & Lukoschus, 1979; *P. minutus japonicus* Uchikawa, 1979; *P. breviatus* Fain & Aellen, 1979*b*; *Pteracaras* sp. 1 (? = *P. mirabilis*, ? = sp G in Dusbábek, 1973); and sp. 2 (Fain & Aellen, 1979*a*). Thus, the 21 named species, several subspecies within four species and a total of 4–7 unnamed species have so far been assigned to the genus *Pteracarus*.

Dusbábek (1973) adopted the chaetotaxy of genu IV and of the female idiosomal dorsum as useful characters in the classification of *Pteracarus*. Using those characters, the 30 full species, that is, 21 known and nine new species, are dividied into three groups as in Table 1. It is an interesting fact that the absence of dorsal seta on genu IV and d_1–d_3 and the presence of d_5 seem to be linked characteristics. On the other hand, mites with a dorsal seta on genu IV bear borsal setae d_1–d_3, with the exception of *P. elegans*, yet presence or absence of d_5 is variable according to species (Table 1). It is still necessary to confirm the presence of a strange setation on the idiosomal dorsum in the female of *P. elegans*, since vestigial d_1–d_3 are often very difficult to observe. Although phylogenetic meanings of differences in the leg and dorsal chaetotaxies are not yet clear, the above grouping of *Pteracarus* species is useful as the first stage of sorting the taxa from one another and for making a key to species.

ACKNOWLEDGEMENTS. Gratitude is expressed to the curators and other staffs of the mammal sections of all the museums listed above for allowing the author to examine the bats deposited in their collections for ectoparasites. Thanks are also due to Mr K. H. Hyatt, Arachnida Section, British Museum (Natural History), for critical reading of the manuscript.

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Manuscript accepted for publication 5 January 1988

Bull. Br. Mus. nat. Hist (Zool.) **55**(1): 109–121 Issued 25 May 1989

Anatomy and phylogeny of the cyprinid fish genus *Onychostoma* Günther, 1896

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INTRODUCTION

Onychostoma Günther, 1896 (type species, *Onychostoma laticeps* Günther= *Barbus simus* Sauvage & Dabry, 1874) is a cyprinid fish genus having its distribution in eastern Asia and is characterized primarily by a broad, inferior mouth with a cornified cutting edge. Since this, so-called 'sector mouth' is also a feature which supposedly characterizes *Varicorhinus* Rüppell, many authors (Nichols, 1925, 1928, 1943; Lin, 1933; Fang, 1940; Wu *et al.*, 1977) have regarded it as a synonym of that genus (type species *Varicorhinus beso* Rüppell). Although Bănărescu (1971) and Taki (1975) have recognised the independent nature of *Onychostoma*, they did not explore the relationship between *Varicorhinus* and *Onychostoma*. Howes (1982) studied the anatomy and evolution of the jaws in 'sector mouth' fishes, including the genera *Cyprinion*, *Varicorhinus*, *Capoeta* and *Onychostoma*. Howes concluded 'in this study the presence of a sector mouth in various cyprinid taxa is seen both as a character indicating relationship (synapomorphy) and as one independently evolved as a parallelism'. The existence of synapomorphic osteological and myological characters indicate *Cyprinion* as a monophyletic group, but '... the phyletic relationship of *Onychostoma*, *Varicorhinus* and *Capoeta* have yet to be determined' (Howes, 1982:320 & 333).

Bănărescu (1971) divided *Onychostoma* into two subgenera, *Onychostoma sensu stricto* and *Scaphesthes* Oshima, 1919 (type species: *Scaphesthes tamusuiensis* Oshima = *Gymnostomus barbatulus* Pellegrin, 1908). Taki (1975) considered *Onychostoma* closely related to *Semiplotus*, *Scaphiodonichthys*, *Scaphiodon* and *Scaphiognathops*, and recognised these genera as an '*Onychostoma*-group'. He also divided *Onychostoma* into two subgenera, *Onychostoma* and *Gymnostomus* Heckel, 1842 (type species: *Gymnostomus ariza*). Wu *et al.* (1977) included *Onychostoma* and *Scaphesthes* as subgenera in the composite genus *Varicorhinus*. They also included some species of *Scaphiodonichthys* in the subgenus *Onychostoma*. Howes (1982) included *Semiplotus* and *Scaphiodonichthys* in the genus *Cyprinion*. None of those authors have established the monophyly of *Onychostoma*, let alone its phylogenetic relationship.

There are presently recognised 14 species in the genus *Onychostoma* (including *Scaphesthes*). A detailed anatomical study of eight species is reported in this paper. The information gained from this study has provided a basis for a discussion of the classification and relationships of *Onychostoma*. I regard the genus *Onychostoma* as belonging to the barbin subgroup of the subfamily Cyprininae *sensu* Howes (1987) (= subfamily Barbinae *sensu* Chen *et al.*, 1984). From this standpoint the phyletic relationships between *Onychostoma* and related genera may be discussed.

METHODS AND MATERIALS

The osteology was studied from alcian-alizarin stained specimens and dry skeletal preparations. Some characters have been examined using dissected specimens.

ABBREVIATIONS. BMNH, British Museum (Natural History); IHAS, Institute of Hydrobiology, Academia Sinica. A = alizarin stained preparation; D = dissected specimen; S = dry skeleton. All specimens are deposited in the British Museum (Natural History).

Acapoeta tanganica (= *Varicorhinus tanganica*) BMNH 1955. 12. 10: 881 (D); 1906. 9. 6: 11 (S); *Barbus barbus* BMNH uncat. (S); *B. bowkeri* BMNH 1962. 8. 28: 8 (S); *B. bynni* BMNH 1861. 9. 9: 65 (S); *B. callensis* BMNH 1869. 1. 29: 4 (S); *B. gregorii* BMNH 1893.12. 2:

36 (S); *B. longiceps* BMNH 1864. 8. 20: 21 (S); *B. luteus* BMNH 1874. 4. 28: 23 (S); *B. oxyrhynchus* BMNH 1906. 8. 25: 17 (S); *B. rocadasi* BMNH 1911. 6. 1: 26 (S); *Capoeta capoeta* BMNH 1968. 12. 13: 405–416 (A, D); 1906. 9. 6: 11 (S); *C. trutta* BMNH 1974. 2. 22: 1374–1377 (D); *Cirrhina jullieni* BMNH 1883. 7. 4: 47 (S); *Cyprinion macrostomus* BMNH 1974. 2. 22: 1177–1179 (A, D); *C. watsoni* BMNH 1889. 2. 1: 379 (D); *Garra quadrimaculatus* BMNH 1902. 12. 13: 420 (S); *Labeo ariza* (= *Gymnostomus ariza*) BMNH 1889. 9. 26: 82 (D); *L. cylindricus* BMNH 1902. 5. 26: 23 (S); *L. niloticus* BMNH unregistered (S); *Onychostoma gerlachi* BMNH 1988. 6. 24: 23–5 (ex. IHAS 66.249 & 261; A, D); *O. lini* BMNH 1988. 6. 24: 13 (ex. IHAS76.IV.6809, D); *O. rhomboides* BMNH 1988. 6. 24: 14–16 (ex. IHAS 58.7.284, 285; A, D); *O. sima* (= *O. laticeps*) BMNH 1969. 4. 15: 110 (S); 1988. 6. 24: 1–3 (ex. IHAS 81. IV. 791, 792; D, A); *Scaphesthes barbatulus* BMNH 1988. 6. 24: 17–19 (ex. IHAS 74. VI. 844, 931; A, D); *S. barbatus* BMNH 1988. 6. 24: 7–12 (ex. IHAS 75. IV. 2439, 440, 270; D, A, A); *S. lepturus* BMNH 1988. 6. 24: 20–22 (ex. IHAS 76. V. 9379, 5085; D, A); *S. macrolepis* BMNH 1988. 6. 24: 4–6 (ex. IHAS 82. V. 2307, 2399; D, A); *Scaphiodonichthys acanthopterus* BMNH 1988. 6. 24: 26–28 (ex. IHAS 78. V. 383, 489; D, A); *Sc. burmanicus* BMNH 1893. 2. 16: 32 (S); 1980. 12. 17: 113–4 (D); *Sc. macracanthus* BMNH 1988. 6. 24: 29 (ex. IHAS 64. 4. 8; D); *Schizothorax prenanti* BMNH 1969. 4. 15: 120 (D); *Sch. richardsoni* BMNH 1881. 9. 2: 85–7 (D); *Semiplotus semiplotus* BMNH 1889. 2. 1: 364 (D); 1889. 2. 1: 369 (S); *Varicorhinus altipinnis* BMNH 1975. 9. 5: 18–19 (D).*V. beso* BMNH 1902. 12. 13: 365–370 (A. D); 1902; 12. 13: 377 (S); *V. macrolepidotus* BMNH 1976. 5. 21: 12–13 (D); *V. maroccanus* BMNH 1972. 9. 13: 1–3 (D); *V. nyassensis* BMNH 1974. 1. 15: 110 (D); *V. ruwenzorii* BMNH 1971. 1. 5: 154–175 (D).

Abbreviations used in the figures

Aa	Anguloarticular
Am	*Adductor mandibulae* muscle
Bo	Basioccipital
Bp	Basioccipital process
Cm	Coronomeckelian bone
Cp	Coronoid process of dentary
De	Dentary
Do	*Dilatator operculi* muscle
Epi	Epioccipital
Exo	Exoccipital
Fr	Frontal
Fsef	Frontal-supraethmoid foramen
Ic	Intercalar
Io	Infraorbitals (numbered)
Lap	*Levator arcus palatini* muscle
Le	Lateral ethmoid
Lo	*Levator operculi* muscle
Me	Mesethmoid
Mp	Masticatory plate
Mx	Maxillary
Nc	Neural complex
Ns	Neural spines
Of	Olfactory foramen
Op	Operculum
Os	Orbitosphenoid
Pal	Palatine
Par	Parietal
Pe	Preethmoid
Pmp	Postero-medial process of symphysial surface of dentary
Pmx	Premaxillary
Pro	Prootic
Ps	Parasphenoid
Pte	Pterotic
Ptf	Posttemporal fossa
Pts	Pterosphenoid
Pty	Pterygiophore (dorsal)
Se	Supraethmoid
Sg	Snout groove
Sj	Synarthritic mandibular joint
Sn	Supraneurals (numbered)
So	Supraoccipital
Sor	Supraorbital
Sp	Sphenotic
Srp	Supraethmoid rostral process
Stf	Subtemporal fossa
Vo	Vomer
Vf	Vomer facet

ANATOMICAL CHARACTERS AND THEIR PHYLOGENETIC SIGNIFICANCE

Cranium

The neurocranium of *Onychostoma sima* is shown in Fig. 1. In general appearance the cranium of *Onychostoma* and *Scaphesthes* is broad and slightly depressed. The posterior part of the cranium (occipital region) is short, being less than one-third of total cranial length. This condition is also found in *Cyprinion*, *Semiplotus* and *Scaphiodonichthys* but in these taxa, the occipital region is even shorter. In *Varicorhinus* and *Capoeta* the neurocranium is more or less narrow and elongate (Fig. 2); its posterior (occipital) part is almost a half the total cranial length, which is regarded as plesiomorphic for cyprinid fishes.

In *Onychostoma sima* (Fig. 1 & Fig. 3), the supraethmoid is broad and short with a medial anterior process. This rostral process is directed ventrally and forms a vertical strut. The medial part of the supraethmoid is deeply depressed and covered with a thick connective tissue. The kinethmoid is rod-shaped and lies along the medial depression of the supraethmoid. The mesethmoid is very short and hardly protrudes beyond the anterior border of the supraethmoid. Antero-ventrally the mesethmoid forms a surface that provides part of the preethmoid fossa. The notched posterior border of the mesethmoid forms part of the olfactory foramen. There are two pairs of preethmoids in *Onychostoma sima*, a condition comparable to that in *Cyprinus*; a thick cartilage pad separates the preethmoid and the maxillary process. Each well-developed lateral ethmoid (Fig. 4a) forms a triangular wall, the ventral border of which is almost on the same horizontal level as the vomer. It is more or less compressed and has only a moderately-developed facet articulating with the entopterygoid. The palatine (Fig. 5a) is short and compressed, its antero-ventral process articulates directly with the vomer. The vomer (Fig. 1 & Fig. 6a) is short, its posterior margin extending to a line level with that of the lateral ethmoid walls; anteriorly it curves ventrad and has a slight transverse convexity. Antero-laterally it is produced into a wedge-shaped platform which provides the lower part of the preethmoid fossa. Below the preethmoid there is a small facet (Fig. 6a, Vf) into which articulates the palatine.

In all species of *Onychostoma* and *Scaphesthes*, whether the mouth is wide or narrow (see below), the condition of the ethmo-vomerine region is structurally the same as in *Onychostoma sima*. *Cyprinion*, *Semiplotus* and *Scaphiodonichthys* also possess a broad supraethmoid with ventrally directed rostral process. In *Semiplotus semiplotus* and *Scaphiodonichthys burmanicus*, the supraethmoid is very short and almost vertically aligned. There is a foramen between the frontals and the supraethmoid (Howes, 1982). In the wide-mouth species of *Onychostoma*, *Scaphesthes* and in the other taxa mentioned the palatines are more compressed (Fig. 5b,c). The vomers are more or less hypertrophied with a flat anterior border; all species of these taxa possess a facet with

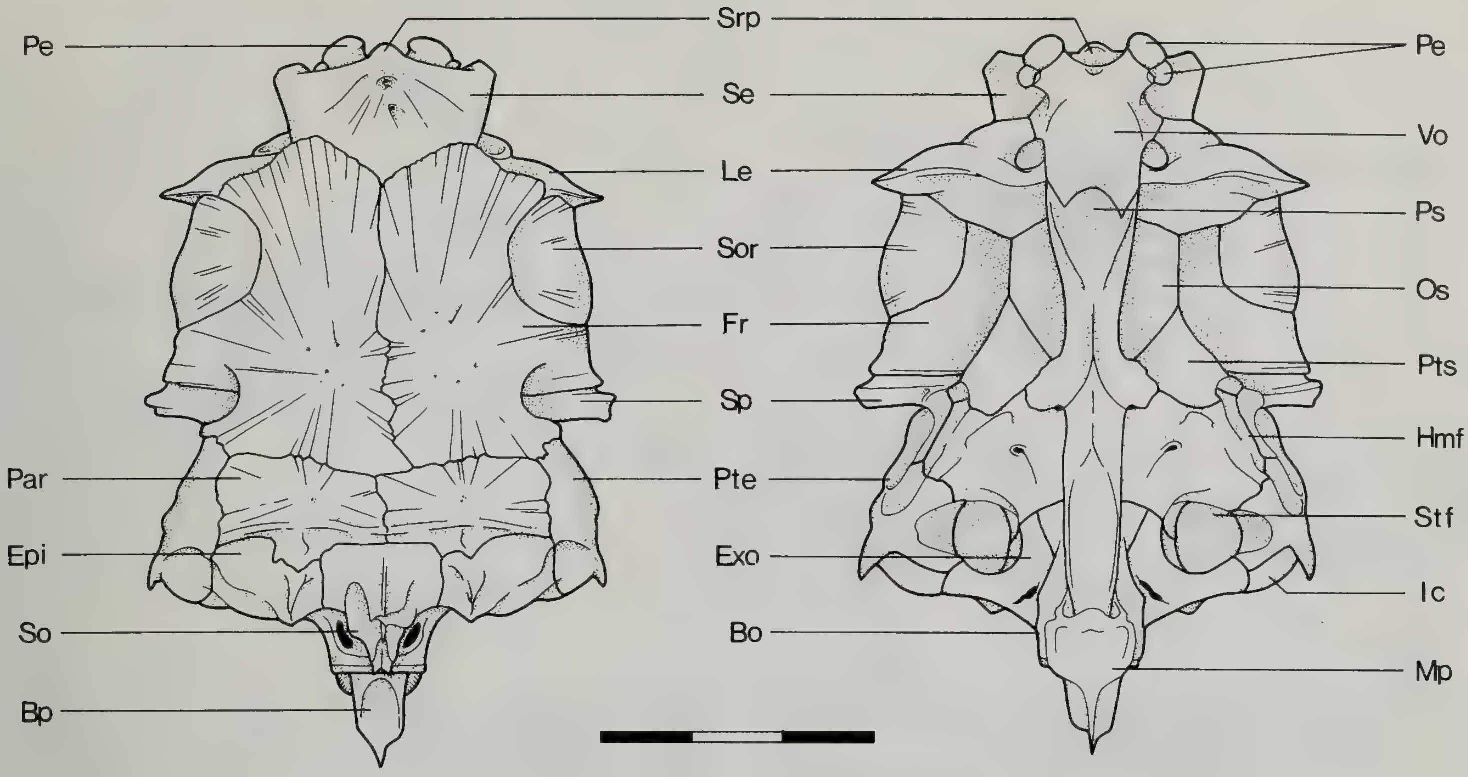
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Fig. 1 Neurocranium of *Onychostoma sima* in dorsal (left) and ventral (right) views

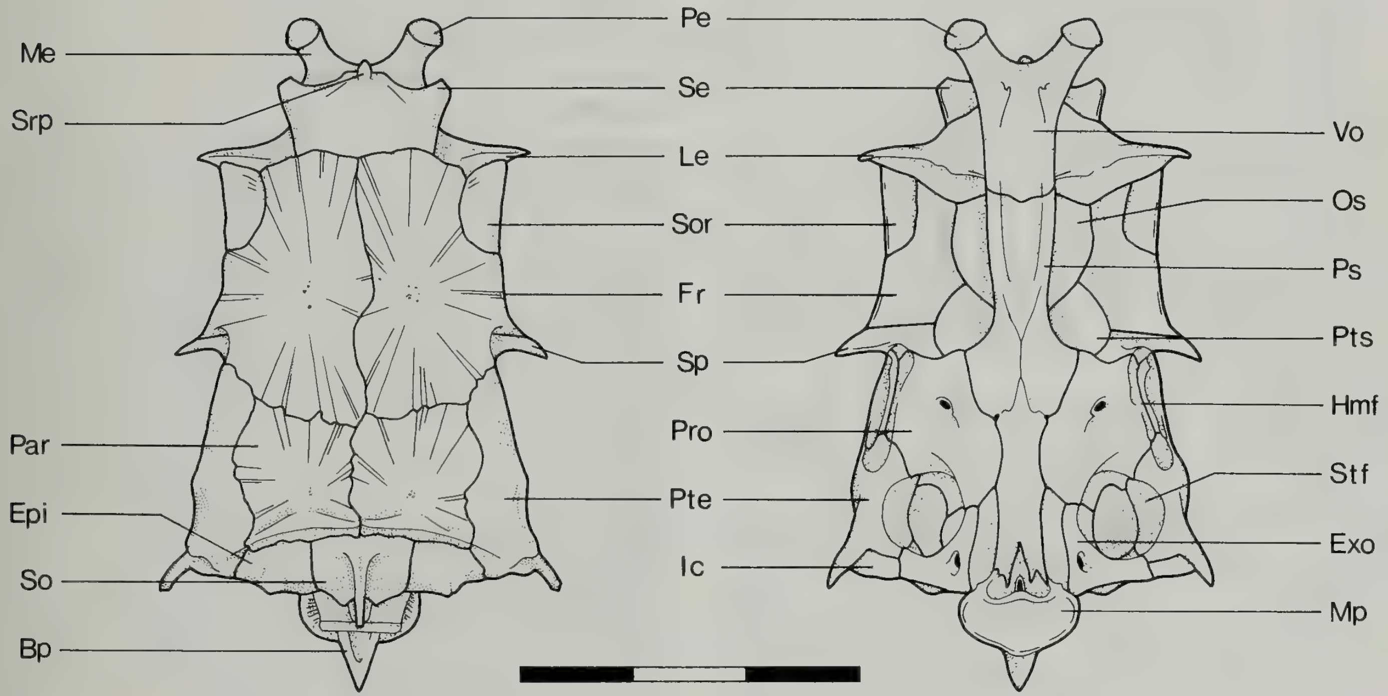
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Fig. 2 Neurocranium of *Varicorhinus beso* in dorsal (left) and ventral (right) views

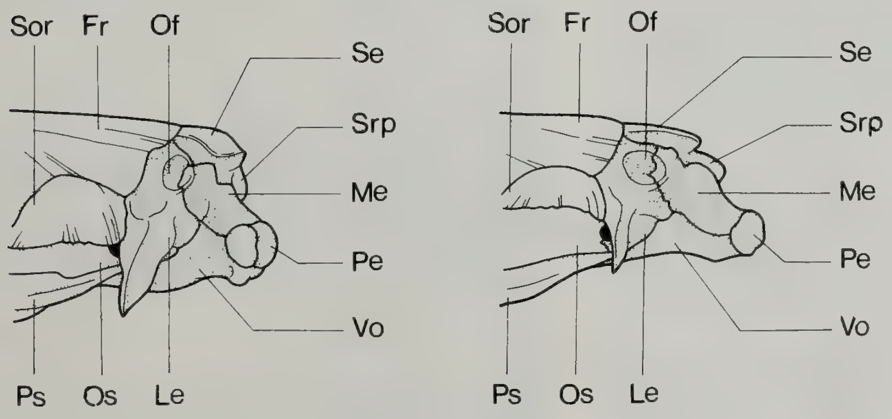
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Fig. 3 Ethmo-vomerine regions in lateral view:
(left) *Onychostoma sima*
(right) *Varicorhinus beso*

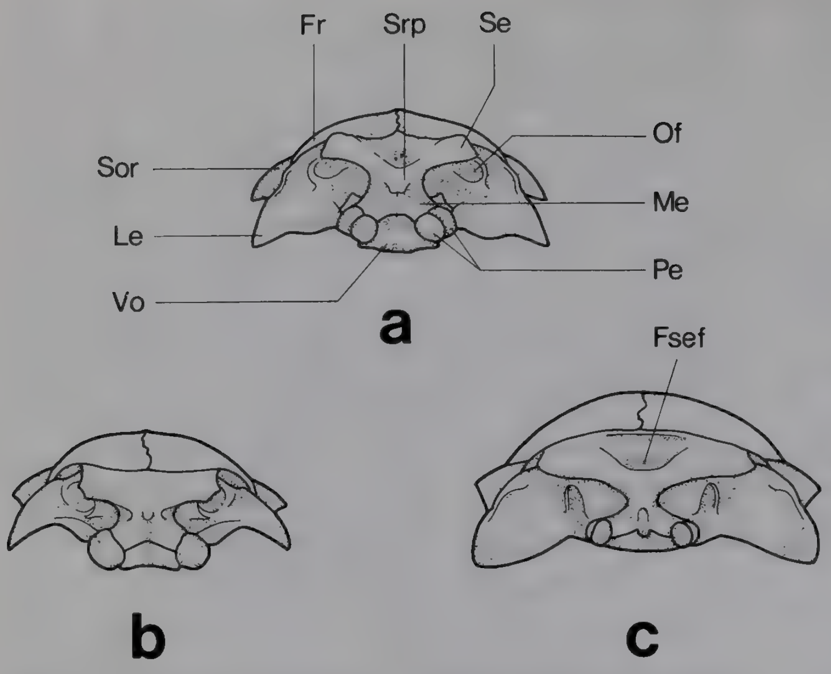

Fig. 4 Neurocranium in anterior view:
a. *Onychostoma sima*
b. *Varicorhinus beso*
c. *Scaphiodonichthys burmanicus*

which articulates the palatine; in some, such as *Semiplotus semiplotus*, the facet is well-developed.

In *Varicorhinus beso* (Fig. 2 & Fig. 3) the supraethmoid is broad with a small medial anterior process. The rostral process is directed anteriorly. Compared with *Onychostoma* the mesethmoid is slightly longer and protrudes anteriorly below the supraethmoid; the vomer is V-shaped, thinner and laterally it forms a wedge-shaped platform which provides the lower part of the preethmoid fossa. The anterior border of the vomer and the mesethmoid are concave and bear a wide groove to accommodate the rod-shaped kinethmoid. The ventral surface of the vomer lacks a palatine articulatory facet, but bears two small process on either side of the midline to which the palatine ligament attaches. In contrast to *Onychostoma* the lateral ethmoid wings have a concave ventral margin, lie above the horizontal plane of the vomer and are thinner (Fig. 4b).

No distinct differences have been found in the *orbital region* between *Onychostoma*, *Varicorhinus*, *Cyprinion*, *Scaphesthes*, *Scaphiodonichthys* and *Semiplotus*. In these genera the frontals are all broad; the supraorbital bones are large; the orbitosphenoids are deep and ventro-medially they are joined to form a thick interorbital septum which contacts the parasphenoid. The pterosphenoids provide the walls of the optic foramen and the anterior part of the posterior myodome. Posteriorly each pterosphenoid is bordered by the sphenotic and the prootic and does not contact the ascending wing of the parasphenoid. The parasphenoid is horizontally aligned; anteriorly it narrows, then widens and becomes concave where it overlies the vomer; posteriorly each broad ascending wing contacts the respective prootic. The midline ridge of the parasphenoid is well-developed in most species of the above named genera, but in a few (e.g. *Cyprinion watsoni*) it is not distinct.

The *otic region* is short in *Onychostoma* (Fig. 1), *Scaphesthes*, *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*. The parietals and the prootics are short, deep and almost rectangular. Each sphenotic projects laterally as a spinous or broad ledge, at the ventral base of which there is a large depression which forms the antero-lateral part of the hyomandibular fossa. The prootic forms the lateral boundary of the anterior hyomandibular fossa and the anteromesial boundary of the subtemporal fossa. The subtemporal fossa is deep with an anterior cavity; its outline is elliptical, with the long axis transverse. The inner wall of the fossa is formed by the prootic, and the outer by the pterotic; the posterior wall by the pterotic and the exoccipital; the epioccipital forms the roof of the fossa. The pterotic is short and broad; anteroventrally it houses the greater portion of the posterior hyomandibular fossa. Its ventromedial surface contains the outer part of the subtemporal fossa, which forms a U-shaped depression, and its dorsal surface forms the lateral wall of the posttemporal fossa. In *Onychostoma*, *Scaphesthes*, *Scaphiodonichthys* and *Semiplotus*, the posttemporal fossae (Fig. 7 a, b) are very deep, the anterior border of the fossa extends almost to the frontal. In these taxa the roof of the posttemporal fossa is formed by the parietal and the medial wall from the exoccipital. However, in *Cyprinion* (Fig. 7d) the posttemporal fossae are shallower and open into the subtemporal fossae; the parietals contribute only a small portion anteriorly to the posttemporal fossae. Although the basioccipital (masticatory) plate is entirely absent in *Scaphiodonichthys burmanicus* (Howes, 1982), the ventral surface of the pharyngeal process is expanded into a triangular masticatory plate in all species of *Onychostoma* and *Scaphesthes*, and in *Scaphiodonichthys acanthopterus* and *S. macracanthus*.

In contrast to the above cited genera *Varicorhinus beso* (Fig. 2) has a square parietal, an elongate prootic and a circular subtemporal fossa. The pterotics are elongate and ventro-medially contain the lateral part of the subtemporal fossa which is a broadly curved depression. The posttemporal fossae (Fig. 7c) are shallower and open into the subtemporal fossae.

Mouth and jaw

Howes (1982) gave a detailed anatomical description of the jaw structure of *Semiplotus semiplotus* and compared it with that of *Onychostoma*, *Varicorhinus*, *Capoeta* and *Cyprinion*. A significant character of the lower jaw in *Semiplotus*, *Cyprinion* and *Scaphiodonichthys* is a synarthritic dentary joint (Fig. 8b). *Onychostoma*, *Scaphesthes*, *Varicorhinus* and *Capoeta* all lack this feature, but in *Onychostoma* and *Scaphesthes* a strong process stems from the medial symphysial surface and curves posteromedially (Fig. 8a). A thick ligament connects the process with its partner. Such a process is

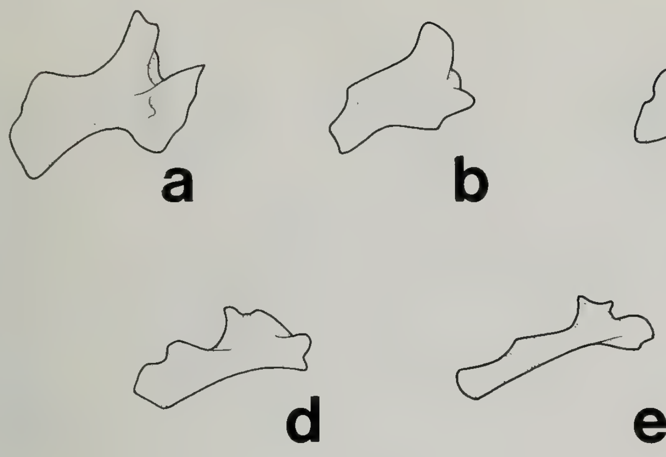

Fig. 5 Dorso-anterior view of the right palatine in:
a. *Onychostoma sima*
b. *Scaphesthes barbatulus*
c. *Scaphiodonichthys burmanicus*
d. *Varicorhinus beso*
e. *Barbus barbus*

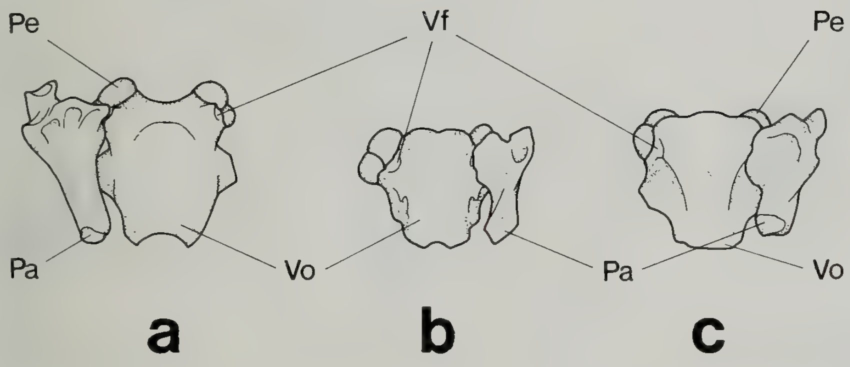

Fig. 6 Ventral view of vomer and palatine in:
a. *Onychostoma sima*
b. *Scaphiodonichthys burmanicus*
c. *Semiplotus semiplotus*

lacking in *Varicorhinus* and *Capoeta*. In these genera, the dentaries contact one another across a flat symphysial surface and there is no inner ligament (Fig. 8c).

The mouth of *Onychostoma* and *Scaphesthes* exhibits three external morphotypes. In type one (Fig. 9a) the mouth width spans that of the head; this type is present in *Onychostoma sima*, *O. elongatus*, *O. angustistomatus* and *Scaphesthes macrolepis*. In type two (Fig. 9b) the mouth width is greater than that of the head (the corners of the mouth are expanded beyond the lateral margin of the head); it is present in *Scaphesthes barbatulus*, *S. alticorpus*, *S. lepturus* and *Onychostoma gerlachi*. In type three (Fig. 9c) the mouth is moderate to small, its width less than that of the head; this type is present in *Onychostoma lini*, *O. ovalis*, *O. rhomboides* and *Scaphesthes barbatus*. Despite these external differences, all these taxa possess the derived osteological structures of the jaws described for *Onychostoma laticeps* (see above and Howes, 1982).

The mouth of *Scaphiodonichthys* belongs to type two category, but lacks the lateral groove that runs from the snout to the angle of the mouth (Fig. 10) and which is present in *Onychostoma* and *Scaphesthes*. The 1st and 2nd infraorbitals entirely cover the maxilla and premaxilla laterally. The *adductor mandibulae* muscle A_1 inserts on the posterior tip of the maxilla (Fig. 11b). In the majority of cyprinids, including *Onychostoma*, *Scaphesthes*, *Varicorhinus*, *Cyprinion* and *Semiplotus*, the snout groove is present and the *adductor mandibulae* muscle A_1 inserts on a small centrally situated lateral process on the maxilla (Fig. 10 & 11, a,c,d).

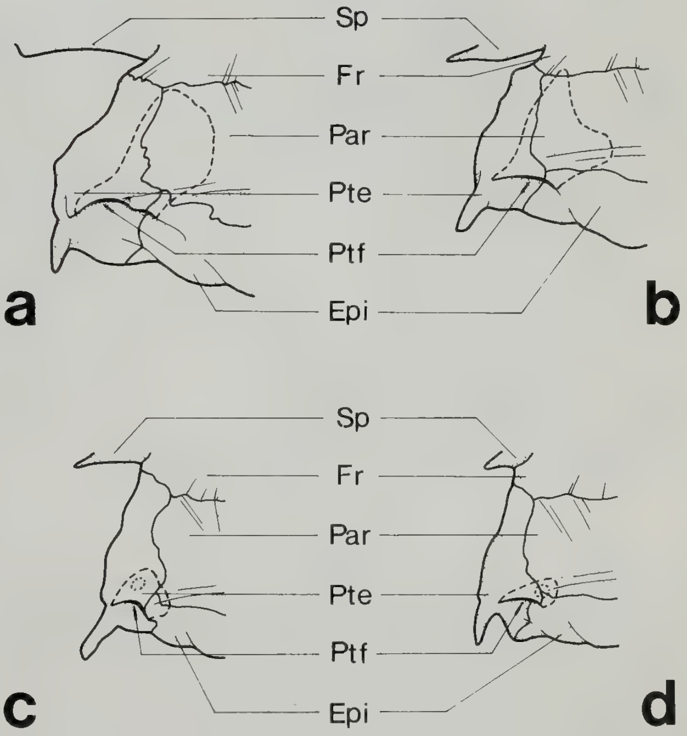

Fig. 7 Pterotic region in dorsal view to show the posttemporal fossa of:
a. *Onychostoma sima*
b. *Scaphiodonichthys burmanicus*
c. *Varicorhinus beso*
d. *Cyprinion watsoni*

Circumorbitals

Although the supraorbital is large in *Onychostoma sima* (Fig. 1 & Fig. 12), it is widely separated anteriorly from the first infraorbital (lachrymal) and posteriorly from the 5th infraorbital, as in most barbins. The lachrymal is a deep pentagonal bone; its inner face attaching to the mid-lateral ascending

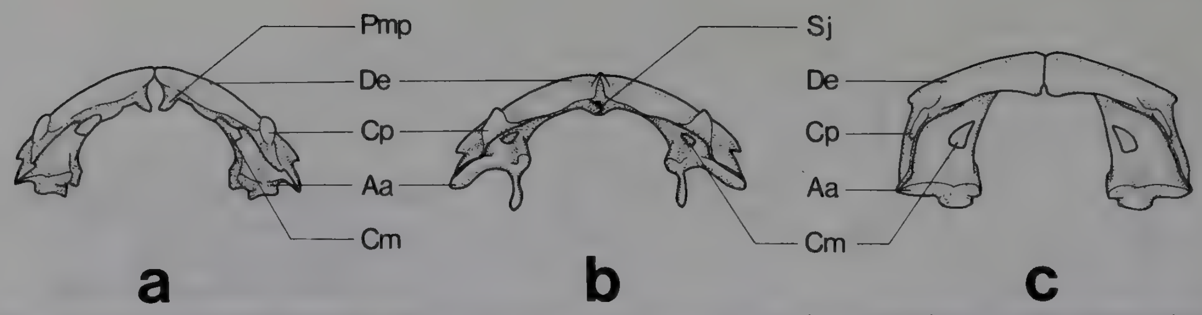

Fig. 8 Lower jaw bones in dorsal view of: a. *Onychostoma sima*; b. *Semiplotus semiplotus*; c. *Varicorhinus beso*.

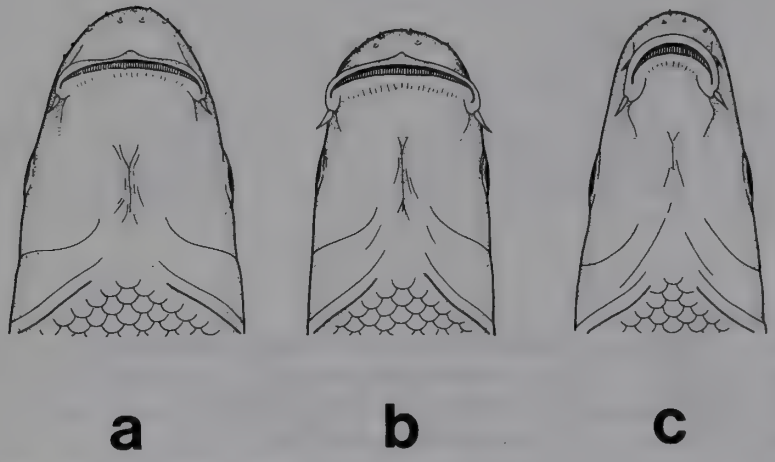

Fig. 9 Ventral view of the heads in:
a. *Onychostoma sima*
b. *Scaphesthes barbatulus*
c. *Scaphesthes barbatus*

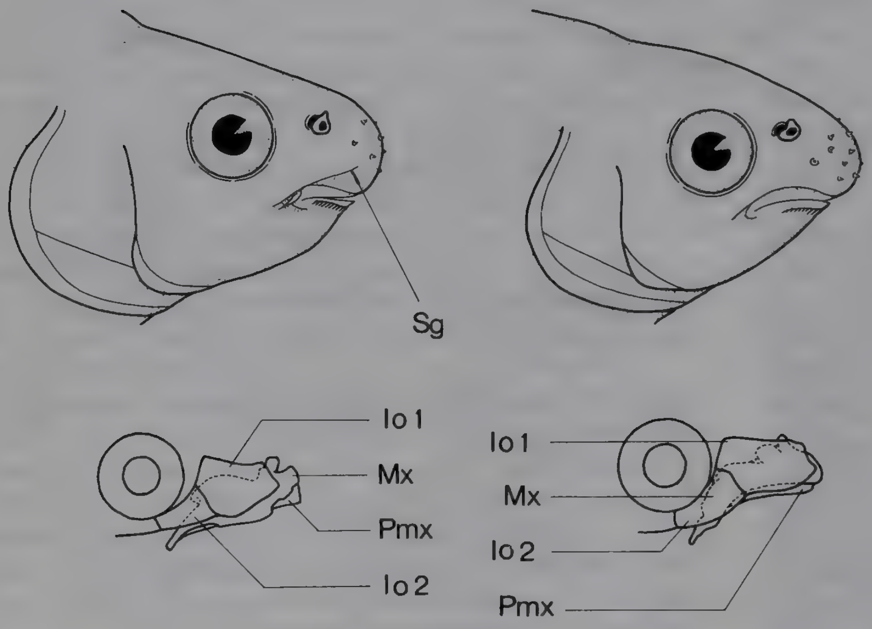

Fig. 10 Lateral view of head and infraorbital bones of:
(left) *Onychostoma sima*
(right) *Scaphiodonichthys burmanicus*

maxillary process *via* tendinous tissue. The sensory canal runs through the ventral part of the lachrymal. The other infraorbitals are narrow and the sensory canal runs along their dorsal rim. The 5th infraorbital is reduced to a bony tube which extends dorso-posteriorly and does not contact the lateral process of the sphenotic. There are thus large gaps between the 5th infraorbital and the sphenotic, and the 5th infraorbital and the opercular process. Almost all of the *dilatator operculi* muscle is exposed. There is also a wide gap between the pterotic and dorsal border of the operculum and the *levator operculi* is well-developed. The condition of the circumorbitals in all species of *Onychostoma* and *Scaphesthes* is the same as described for *O. sima*.

In *Varicorhinus beso* (Fig. 12) the lachrymal is also a deep pentagonal bone but the sensory canal runs centrally through the bone; the anterior part of the sensory canal runs close to the bone's anterior border. The 2nd and 3rd infraorbitals are shallow but the 4th and 5th infraorbitals are deep. In some species of *Varicorhinus*, e.g. *V. ruwenzorii* (Fig. 13a) and *V. macrolepidotus*, the 4th and 5th infraorbitals are apparently fused (in some specimens of *V. beso* both the 4th and the 5th may be present on one side only). The upper infraorbital is never reduced and contacts the lateral process of the sphenotic and the opercular process. The *dilatator operculi* muscle is almost covered completely by the infraorbital, and the upper gap between the pterotic and the opercular border is very narrow.

The shape of the lachrymal is variable in the barbins (Howes, 1987) and it is difficult to evaluate it as a phylogenetic character. In most barbins (Fig. 13a–j) the 4th infraorbital is not reduced and the 5th infraorbital is never reduced to only the sensory canal and it always contacts the lateral process of the sphenotic. *Cyprinion* and *Semiplotus* (Fig. 13i,j) both possess this morphology, which, from its widespread distribution appears

Table 1 Vertebrae, lateral line scales and branched rays counts in some examined species

Species	Vertebrae		Lateral line scales	Branched rays	
	Total	Pre-dorsal		Dorsal	Anal
Onychostoma sima	44	11	45–48	8	5
O. gerlachi	45	11	46–49	8	5
O. lini	45	11	47–49	8	5
O. rhomboides	42	10	42–45	8–9	5
Scaphesthes barbatulus	44	12	44–47	8	5
S. macrolepis	48	14	50–53	8	5
S. barbatus	45	12	47–48	8	5
S. lepturus	43	11	44–48	8	5
Scaphiodonichthys burmanicus	41	11	37–38	9–10	5
S. acanthopterus	42	11	41–42	11–12	5
S. macracanthus			42–44	13–14	5
Semiplotus semiplotus	38	9	30–31	24–28	8–10
Cyprinion macrostomus	40	11	37–41	13–16	7
C. watsoni	38	11	37–40	9–11	7
C. microphthalmum	37	11	37–40	10–11	7
Varicorhinus beso	42	10	30–35	9–10	5
V. tanganicus	44	12	64–70	8–9	5

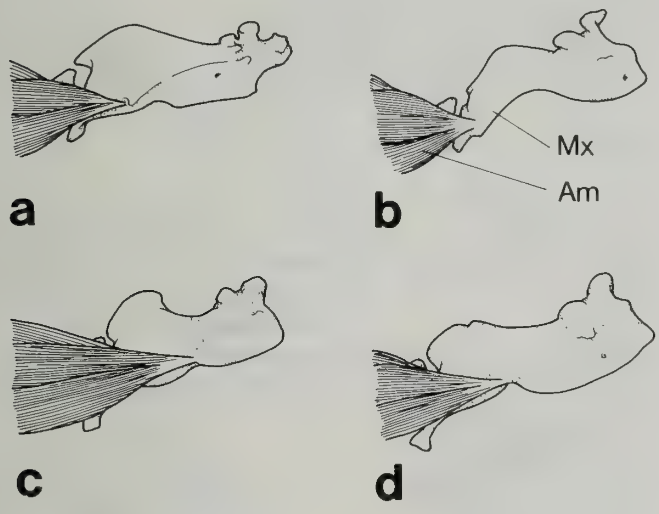

Fig. 11 Insertion of *adductor mandibulae* muscle to upper jaw in:
a. *Onychostoma sima*
b. *Scaphiodonichthys burmanicus*
c. *Cyprinion macrostomus*
d. *Varicorhinus beso*

to be the plesiomorphic condition. Only *Scaphiodonichthys* and *Schizothorax* (Fig. 13k,l) share the supposedly derived infraorbital morphology of *Onychostoma* and *Scaphesthes*.

Vertebral column and dorsal fin

In *Onychostoma sima* (Fig. 14a) the neural complex is tall and axe-shaped with a forwardly inclined anterior border and widely separated from the supraoccipital as in most barbins. The posterior border of the neural complex is slightly concave and widely separated from the posteriorly inclined 4th neural spine, which is less than a half its height. There are 7 supraneurals between the neural complex and the first dorsal pterygiophore. Each supraneural is a lamellar, triangular, poorly ossified bone narrowly separated from each of those adjacent, their dorsal borders forming an almost continuous bony ridge along the midline of the body. The anterior neural spines are tall and slender.

In *Scaphesthes barbatulus* (Fig. 14b) the neural complex is low with irregular anterior and posterior borders. The 4th neural spine is short and widely separated from the posterior border of the neural complex. There are 8 stick-like supraneurals of irregular size between the neural complex and the first dorsal pterygiophore.

These two morphotypes of the vertebral column are present in species of *Onychostoma*, *Scaphesthes* and *Cyprinion*. That described for *O. sima* is also found in *O.* gerlachi, *O. rhomboides*, *S. lepturus*, *C. macrostomus* and *C. watsoni*; that for *S. barbatus* is also found in *S. macrolepis* and *O. lini*.

Howes (1982) described the anterior vertebral column of *Semiplotus semiplotus* and *Scaphiodonichthys burmanicus*. In the former, the supraneurals are enlarged, articulating with each other and overlapping the neural complex and the first dorsal pterygiophore. In the latter taxon (Fig. 14c) the supraneurals are also sequentially joined and overlap the anterior margin of the 1st dorsal pterygiophore. The anterior margins of the neural spines are produced to form a flange which articulates with the base of each supraneural.

In *Varicorhinus beso* (Fig. 14d) the neural complex is also tall and axe-shaped as *Onychostoma sima*, but the 4th neural spine is vertically inclined and close to the posterior border of the neural complex. There are only six supraneurals which are enlarged and articulate with one another, the last element contacts the 1st dorsal pterygiophore.

In the Cyprininae, the vertebral number is variable, with a modal range of 38–40 (Howes, 1987). However, the total vertebral number of *Onychostoma* and *Scaphesthes* is 42–48 and is higher than that of most barbins, but the pre-dorsal vertebral number is only 10–12 (with the exception of *Scaphesthes macrolepis* which has 14). The lateral line scales number 42–53. In *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*, the total number of the vertebrae and the lateral line scales are all lower than those of *Onychostoma* and *Scaphesthes*, but the number of predorsal vertebrae is similar in all genera. In view of its restricted distribution, I consider a high total number of vertebrae as a synapomorphy for *Onychostoma* and *Scaphesthes* (Table 1).

The number of the dorsal and anal fin rays is stable in *Onychostoma* and *Scaphesthes* (Table 1). There are 8–9 branched dorsal fin rays and 5 branched anal fin rays in these two genera which are the plesiomorphic numbers for cyprinines. In *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*,

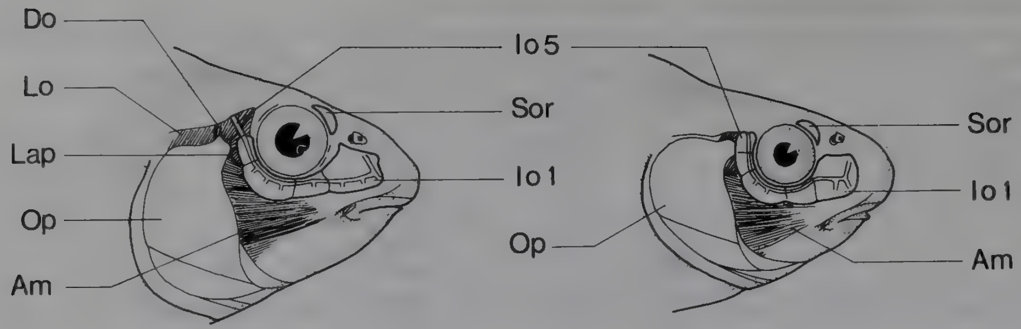

Fig. 12 Circumorbital series of: (left) *Onychostoma sima* (right) *Varicorhinus beso.*

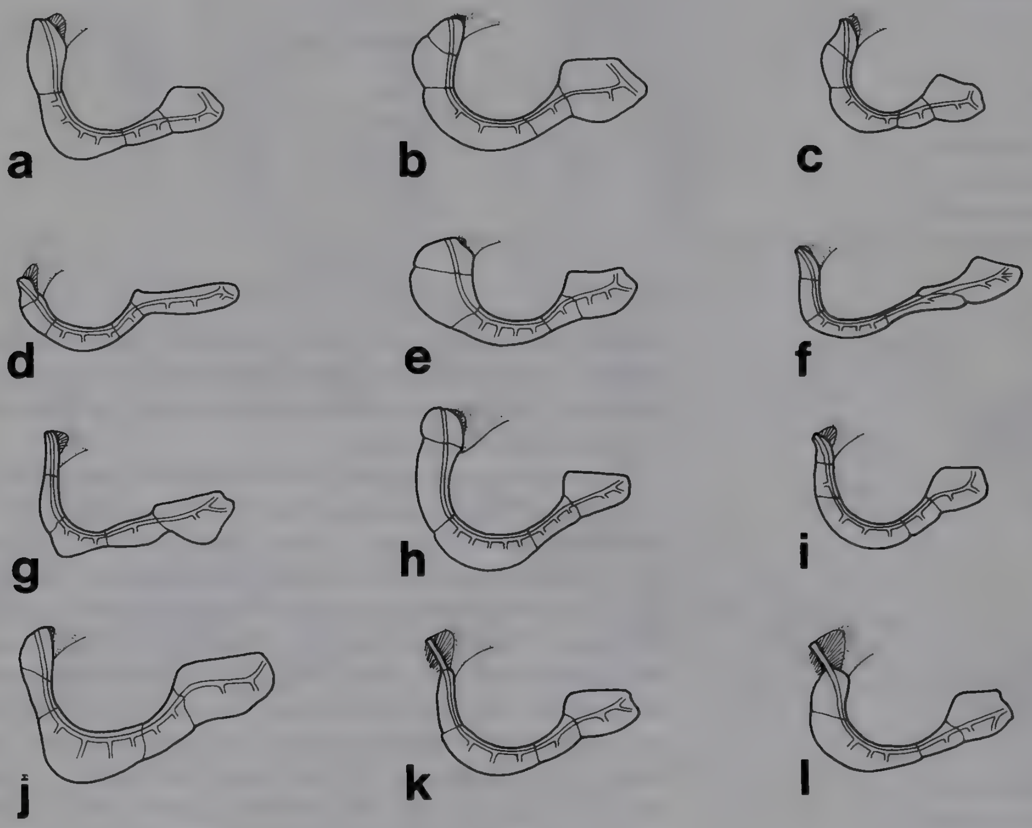

Fig. 13 Infraorbital series of:

a. *Varicorhinus ruwenzorii*
b. *Varicorhinus albpinnis*
c. *Capoeta capoeta*
d. *Barbus barbus*
e. *Barbus luteus*
f. *Labeo cylindricus*
g. *Garra quadrimaculatus*
h. *Cirrhina jullieni*
i. *Cyprinion macrostomus*
j. *Semiplotus semiplotus*
k. *Scaphiodonichthys burmanicus*
l. *Schizothorax richardsoni.*

however, the number of the rays of the dorsal or anal fin is higher and variable (Table 1) and is considered an apomorphic condition.

In the Cyprininae, the last unbranched dorsal fin ray varies from being flexible to heavily ossified and may be smooth or serrated along its posterior margin. This condition is also found in *Cyprinion* (including *Semiplotus* and *Scaphiodonichthys*). Whereas in *Varicorhinus* the posterior margin of the last unbranched dorsal fin ray is smooth, it may be also flexible or heavily ossified. Although the posterior margin of the last unbranched dorsal fin ray is serrated in *Onychostoma*, the ray is more or less flexible and segmented; it is never fully ossified. In some species, *Onychostoma lini*, the last unbranched dorsal fin ray is slender and serrations are not apparent (Fig. 15).

DISCUSSION

Phylogenetic position of the genus *Onychostoma*

From the foregoing descriptions and analyses, no synapomorphic characters can be found in *Onychostoma* (including *Scaphesthes*) and *Varicorhinus* except the possession of a sharp, horny edge to the lower jaw. Howes (1982) regarded this feature in both taxa as a parallelism. *Varicorhinus* possesses many plesiomorphic characters in common with *Barbus* sensu lato; although Howes (1982) has suggested that *Varicorhinus* forms a close relationship with African *Barbus*.

Characters identified as apomorphic in *Onychostoma* also occur in *Scaphesthes*, *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*. The synapomorphies which serve to identify these taxa as a monophyletic group are:

1. Supraethmoid broad and short, its rostral process ventrally directed; the medial part of the dorsal surface depressed and covered with a thick connective tissue.
2. Vomer provides a facet articulating with the short and compressed palatine.
3. Parietal and prootic short and deep almost rectangular.
4. Pterotic short and broad, ventrally containing the lateral part of the subtemporal fossa as a U-shaped depression.
5. Subtemporal fossa is ellipsoidal and deep.

Howes (1982) identified a series of synapomorphic characters possessed by *Cyprinion*, *Semiplotus* and *Scaphiodonichthys* and thus treated these taxa as a single genus, *Cyprinion*. The principal synapomorphy is the presence of a synarthritic dentary joint. *Onychostoma* and *Scaphesthes* both lack this significant feature, but possess a strong medial, posteriorly directed process on the symphysial surface of the dentary.

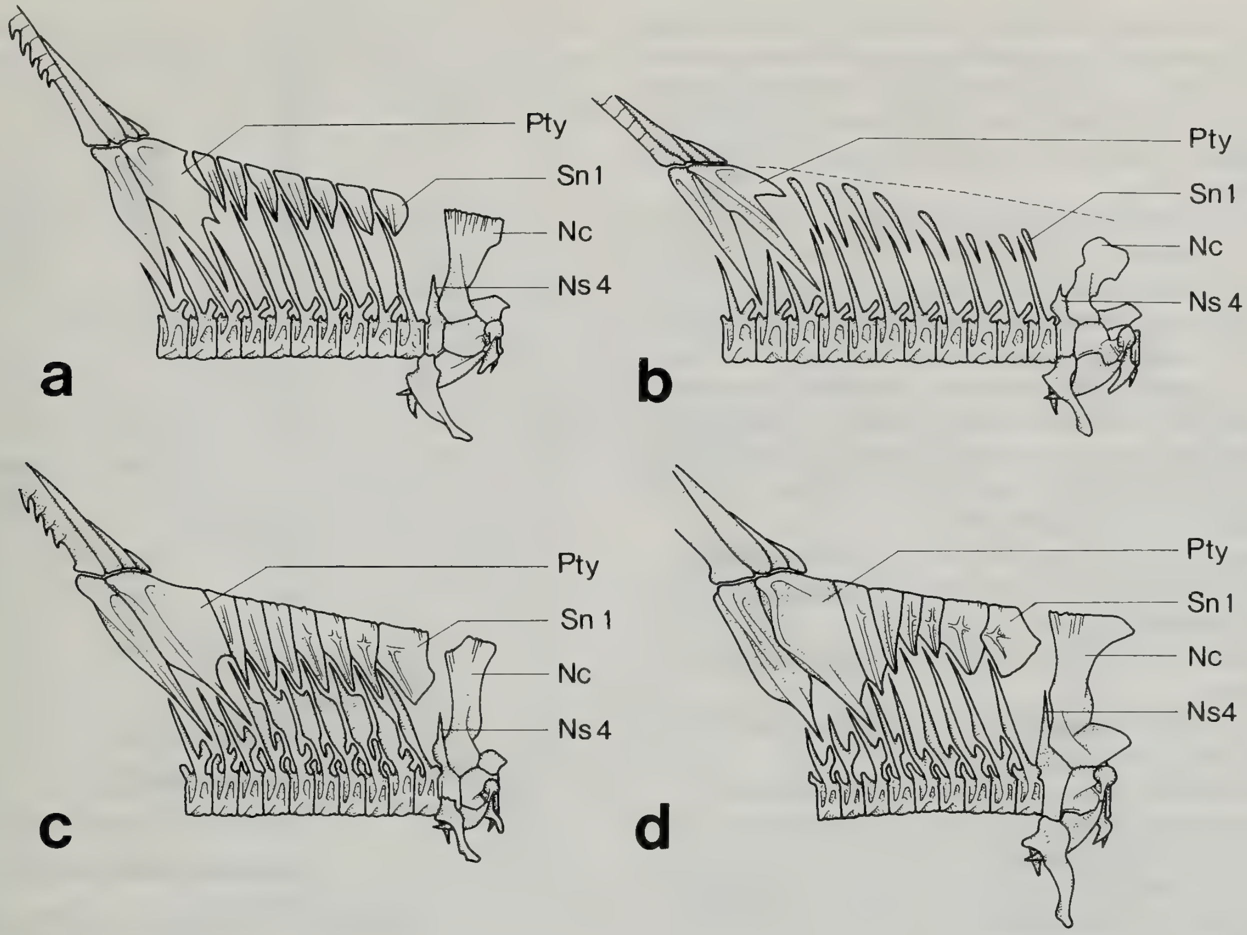

Fig. 14 Anterior vertebral column of: a. *Onychostoma sima*; b. *Scaphesthes barbatulus*; c. *Scaphiodonichthys burmanicus*; d. *Varicorhinus beso*.

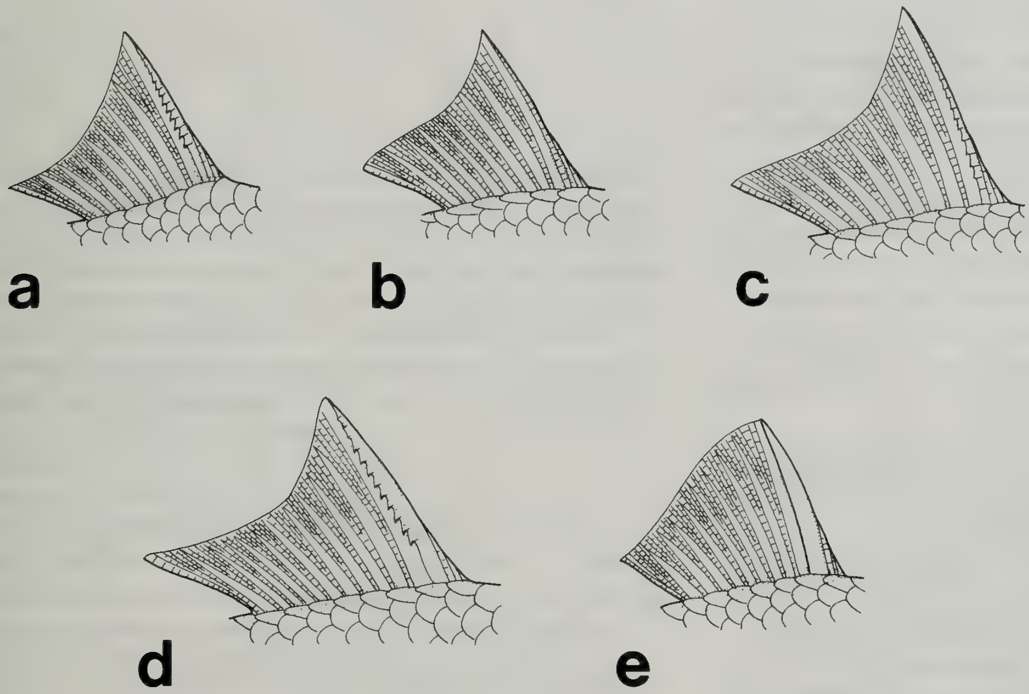

Fig. 15 Dorsal fins of:
a. *Onychostoma sima*
b. *Scaphesthes barbatulus*
c. *Onychostoma lini*
d. *Scaphiodonichthys burmanicus*
e. *Varicorhinus beso*.

This feature is not found in other 'sector mouth' taxa and is thus identified as an apomorphic character.

Scaphiodonichthys possesses a series of autapomorphic characters: it lacks a snout groove; the 1st and 2nd infraorbitals cover the maxilla and the premaxilla; the *adductor mandibulae* muscle inserts on the posterior tip of the maxilla and the pre-dorsal neural spines are extended. There are two characters shared by *Onychostoma* and *Scaphiodonichthys*, one of which is the reduced 5th infraorbital; the other is the anal fin with 5 branched rays. The latter is a plesiomorphic character in cyprinines, but the former is an apomorphic character restricted to these two taxa. However, in view of the conflicting nature of other synapomorphies which support the monophyly of *Scaphiodonichthys*, *Semiplotus* and *Cyprinion* it would appear that this character is homoplastic.

Semiplotus shares many apomorphies with *Cyprinion* and *Scaphiodonichthys* and possesses several autapomorphies (Howes, 1982). It also shares with both *Scaphiodonichthys* and *Onychostoma* a deep posttemporal fossa. It may be argued that since this character is present in all three taxa but absent in *Cyprinion* it has been lost in that genus. However, since it appears that *Cyprinion* is the plesiomorphic member of the triad of *Cyprinion*, *Semiplotus* and *Scaphiodonichthys* then it would presumably possess this feature in one or more of its derived species. As it does not, I apply the more parsimonious argument that it too is a homoplasy between, on the one hand *Semiplotus* and *Scaphiodonichthys*, and on the other *Onychostoma*.

Howes (1982) preferred to regard *Scaphiodonichthys* and *Semiplotus* as synonyms of *Cyprinion*, but was unable to determine the sister-group relationship of *Cyprinion*. It is clear that this lineage is *Onychostoma*, but since this genus shares some of those features which are distributed amongst '*Cyprinion*', it appears taxonomically justifiable to regard *Scaphiodonichthys*, *Semiplotus* and *Cyprinion* of equal (generic) rank. The alternative would be to include *Onychostoma* within *Cyprinion* but this then would not adequately reflect the relationships of the taxa (Fig. 16).

The following characters are identified as synapomorphies for all species of *Onychostoma* and *Scaphesthes*:

1. Vertebral number is 42–48.
2. A strong posteromedial process on the symphysial surface of the dentary.
3. The 5th infraorbital is reduced to a sensory canal and does not contact the sphenotic.
4. Posttemporal fossa is deep and extends to the frontal.

From the foregoing analyses, I consider *Onychostoma* and *Scaphesthes* to be a monophyletic group whose relationship is remote from *Varicorhinus*, but close to *Cyprinion*. I recognize it as the sister-group of the assemblage comprising *Cyprinion*, *Semiplotus* and *Scaphiodonichthys*.

Classification and phyletic relationships within *Onychostoma*

Although at times *Onychostoma* has been regarded as a synonym of *Varicorhinus* all previous authors have recognized it to contain two groups. These groups have been regarded as subgenera *Onychostoma* and *Scaphesthes* (or *Gymnostomus*). The former includes species possessing an osseous and serrated last simple dorsal fin ray, whereas the latter includes those having a flexible and smooth ray. Parenthetically, it should be noted that *Scaphesthes* should be used in preference to *Gymnostomus*, the type species of which, *G. ariza*, has been referred to the genus *Labeo* (Jayaram, 1981).

A comparison between the type species of *Onychostoma* and *Scaphesthes* reveals the following differences:

1. In *Onychostoma sima* the last simple dorsal ray is serrated, but is smooth in *Scaphesthes barbatulus*.
2. In *Onychostoma sima* the mouth width is equal to the head width. In *Scaphesthes barbatulus* the mouth is very wide being greater than the head width.
3. In *Onychostoma sima* the neural complex is tall and axe-shaped; there are 7 triangular supraneurals between the neural complex and the first dorsal pterygiophore. In *Scaphesthes barbatulus* the neural complex is low and there are 8 stick-shaped supraneurals anterior to the dorsal fin.

These three character complexes are, however, irregularly distributed among the species of *Onychostoma* and *Scaphesthes*, and thus cannot be used as diagnostic for either of the two groups.

The last simple dorsal fin ray is never really ossoeus in *Onychostoma*, it is always segmented and flexible at its tip. In *Onychostoma lini* the ray is serrated, but is as slender as that in *Scaphesthes barbatulus*. The use of serrated simple dorsal fin rays as a synapomorphy for *Onychostoma* is thus not justified. According to this character the division of *Onychostoma* into two subgenera is not supported.

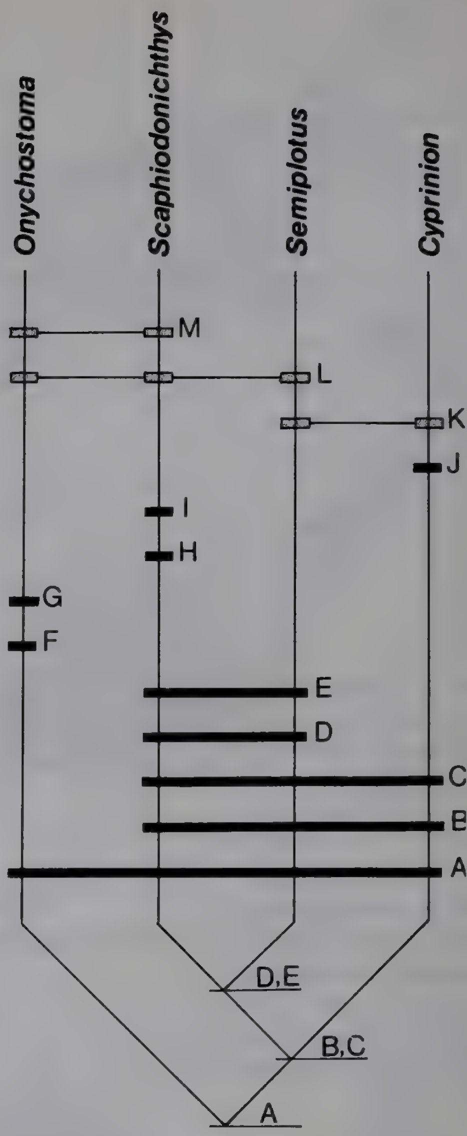

Fig. 16 Cladogram of relationships and apomorphic characters distribution in the *Onychostoma-Cyprinion* group. Level: A. cranial synapomorphies (see text p. 116); B. synarthritic dentary joint; C. branched rays of the dorsal fin; D. jaw synapomorphies (see Howes, 1982); E. cranial synapomorphies (see Howes, 1982); F. mediodorsal process of dentary; G. vertebral number; H. mouth apomorphies; I. extended neural spines; J. expanded pelvic fin rays; K. branched ray of the anal fin; L. posttemporal fossa; M. tubed 5th infraorbitial.

The shape of the neural complex and supraneurals are variable within the Cyprinidae (Howes, 1987). In *Onychostoma* species the development of this character complex is equally variable and it is difficult to evaluate which state of this character is apomorphic. I therefore regard *Scaphesthes* as a junior synonym of *Onychostoma*.

The width of the mouth appears to be a more significant character in diagnosing the genus. On the basis of the various morphotypes (see p. 113) *Onychostoma* species can be placed in three subgroups. Table 2 compares morphological features of all *Onychostoma* species and Figure 17 shows their suggested interrelationships. The polarity of most of these characters cannot be evaluated, thus the scheme presented is classificatory rather than phylogenetic.

Table 2. Comparison of some characters in species of *Onychostoma*. Data presented from Wu *et al.* (1977) and Bănărescu (1971)

Species of *Onychostoma*	Mouth	Lateral line scales	Barbels	Last simple dorsal ray	Neural complex	Caudal peduncle depth in body length	Caudal peduncle depth in its length
barbata	slightly narrow	47–50	present	slender and smooth	low	10.0–12.1	1.5–1.9
lini				slender and serrated			
elongata			absent in adult	strong and serrated		12.6–13.5	3.0
ovalis		42–45	present	strong and serrated		6.8–8.0	1.2–1.5
rhomboides					tall	7.9–8.8	1.4–1.7
rara							
macrolepis	moderate	50–53	present	slender and smooth	low	8.1–10.1	1.3–1.7
sima		44–49	absent in adult	strong and serrated	tall		
angustistomata			present				
brevis				slender and serrated			
barbatula	wide		present	smooth	low	9.1–10.1	1.7–1.8
alticorpus			absent		slender and		
leptura					tall	11.4–14.1	2.0–2.8
gerlachi			absent in adult	strong and serrated			

A synopsis of *Onychostoma* species

Onychostoma Günther, 1896
  Onychostoma Günther, 1896
  Scaphesthes Oshima, 1919
  Scaphiodontella Oshima, 1920
TYPE SPECIES. *Onychostoma laticeps* Günther = *O. sima* (Sauvage & Dabry).

Onychostoma sima (Sauvage & Dabry, 1874)
  Barbus (*Systomus*) *simus* Sauvage *et* Dabry, 1974: 8.
  Onychostoma laticeps Günther, 1896: 211.
DISTRIBUTION. Upper reaches of the Yangtze River and the Pearl River.

Onychostoma angustistomata (Fang, 1940)
  Varicorhinus angustistomata Fang, 1940: 139.
  Varicorhinus szechwanensis Chang, 1944: 44.
DISTRIBUTION. Upper reaches of the Yangtze River.

Onychostoma brevis (Wu & Chen, 1977)
  Varicorhinus (*Onychostoma*) *brevis* Wu & Chen, 1977: 318.
DISTRIBUTION. Upper reaches of the Yangtze River.

Onychostoma macrolepis (Bleeker, 1871)
  Gymnostomus macrolepis Bleeker, 1871: 32.
  Varicorhinus shansiensis Nichols, 1925: 2.
DISTRIBUTION. The Haihe River, Yellow River and Yangtze River.

Onychostoma barbata (Lin, 1931)
  Gymnostomus barbatus Lin, 1931: 113.
DISTRIBUTION. Upper reaches of the Pearl River.

Onychostoma lini (Wu, 1939)
  Varicorhinus lini Wu, 1939: 103.
DISTRIBUTION. Upper reaches of the Pearl River and the Yuanjiang River (a tributary of the Yangtze River).

Onychostoma elongata (Fang, 1940)
  Varicorhinus elongatus Fang, 1940: 138.
DISTRIBUTION. Upper reaches of the Pearl River.

Onychostoma ovalis Pellegrin & Chevey, 1936
  Onychostoma ovalis Pellegrin & Chevey, 1936: 22.
DISTRIBUTION. The Red River.

Onychostoma rhomboides (Tang, 1942)
  Varicorhinus rhomboides Tang, 1942: 156.
DISTRIBUTION. The Pearl River and the Wujiang River (a tributary of the Yangtze River).

Onychostoma rara (Lin, 1933)
  Varicorhinus rarus Lin, 1933: 204.

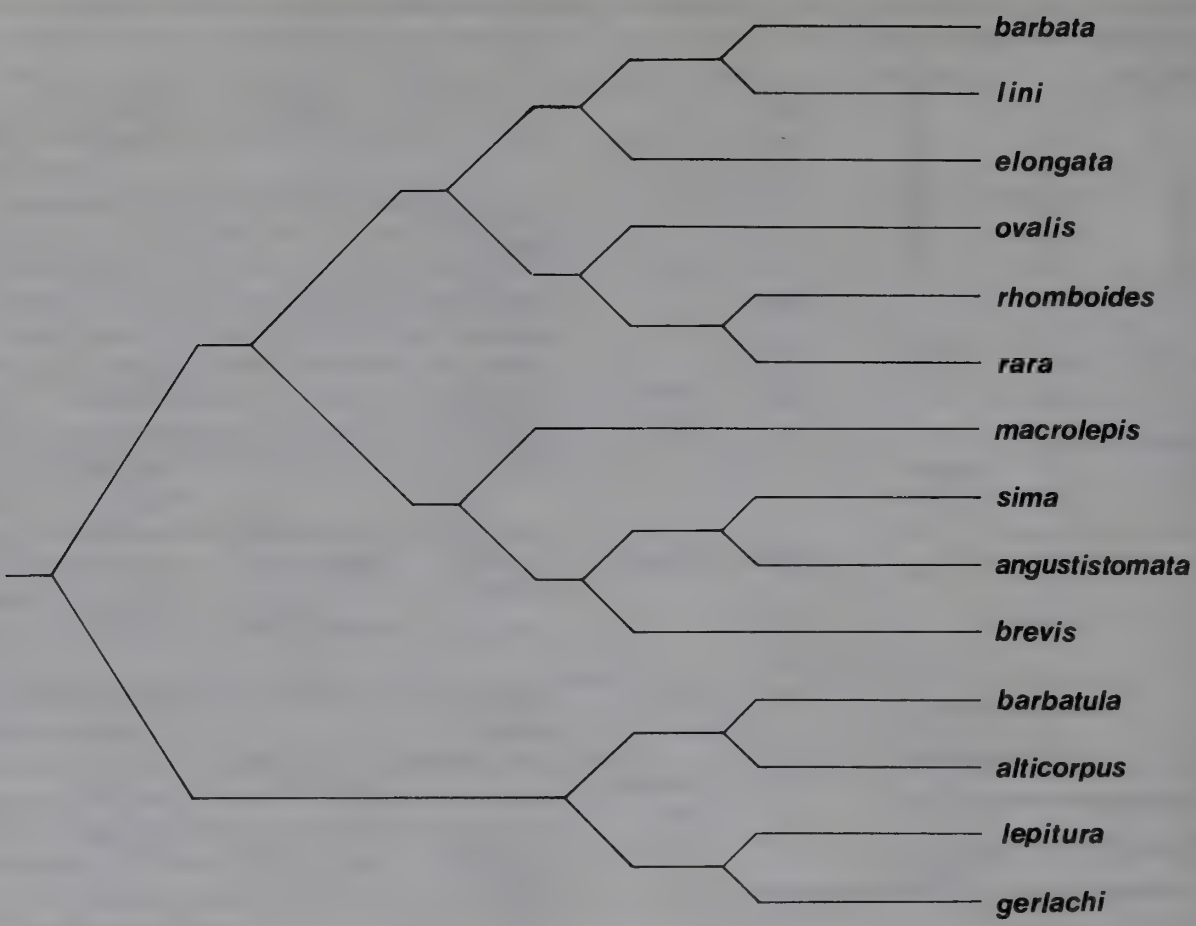

Fig. 17 Dendrogram of *Onychostoma* species based the distribution of the characters listed in Table 2.

DISTRIBUTION. The Pearl River and the Yuanjiang River (a tributary of the Yangtze River).

Onychostoma barbatula (Pellegrin, 1908)
Gymnostomus barbatulus Pellegrin, 1908: 263.
Scaphesthes tamusuiensis Oshima, 1919: 209.
Varicorhinus robustus Nichols, 1925: 2.
DISTRIBUTION. Fujian, Zhejiang and Taiwan Island.

Onychostoma alticorpus (Oshima, 1920)
Scaphiodontella alticorpus Oshima, 1920: 126.
DISTRIBUTION. Taiwan Island.

Onychostoma leptura (Boulenger, 1899)
Gymnostomus lepturus Boulenger, 1899: 961.
DISTRIBUTION: Hainan Island.

Onychostoma gerlachi (Peters, 1880)
Barbus gerlachi Peters, 1880: 1034.
Onychostoma vietnamensis Bănărescu, 1971: 244.
DISTRIBUTION. The Pearl River, the Red River and Hainan Island.

Biogeography of the genus *Onychostoma*

As mentioned above, *Onychostoma* is the sister-group of the complex comprised of *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*. Together these genera form a monophyletic assemblage named as the *Onychostoma-Cyprinion* group. This group is distributed from southeast China, Thailand and Laos, south of Himalaya, to the Arabian Peninsula in the west. Taki (1975) has suggested some dispersal routes to explain the distribution of the *Onychostoma*-group (including *Onychostoma*, *Scaphiodonichthys*, *Scaphiognathops*, *Semiplotus* and *Scaphiodon*). However, it is suggested that the upheaval of the Tibetan Plateau and the Yunnan Plateau before the Pliocene and the presence of pockets of the Tethys Sea during the Pliocene made such dispersal impossible. I consider that the ancestral lineage of the *Onychostoma-Cyprinion* group had been widely distributed throughout central and southern Asia and the vicariant events of plateau formation disrupted this distribution, the consequence being the resultant taxa.

No definitive fossil *Onychostoma* has been found, but many fossil barbin fishes are known from the Miocene from sites in central and eastern Asia. The relationships of these fossils have not been determined and the representative of the ancestral lineage of the *Onychostoma-Cyprinion* group is possibly among them. Among present species of this group, *Onychostoma macrolepis* possesses a number of plesiomorphic characters. For example, the last simple dorsal fin ray is slender and smooth, the dorsal branched rays number 8, the anal 5; the neural complex is low and the supraneurals are stick-like; the mouth is moderate in width and barbels are present. This species occurs in the most northern part of the geographical range of the group. It occurs in the mountain streams of the Haihe River, the Yellow River and the Yangtze River. On account of the cold climate the fish hibernates in burrows from October to April. I consider *Onychostoma macrolepis* to be a relic of the ancestral lineage of the *Onychostoma-Cyprinion* group and assume this lineage to have been widespread in central and eastern Asia before the Pliocene when warmer climates prevailed in this area.

Since the late Tertiary the climate has cooled and the fishes of *Onychostoma-Cyprinion* group supposedly became extinct in the northern part of central and eastern Asia. Some of them may have migrated towards southern Asia following the close of the Tethys Sea. The upheaval of the Tibetan Plateau (including the Yunnan Plateau) forms a barrier between south-western Asia and eastern Asia which would have split the group into two subgroups. The eastern subgroup, *Onychostoma*, never occurs westward beyond the Yunnan Plateau and the Red River. The Yunnan Plateau appears to form a boundary between southern Chinese and south-eastern Asian taxa of many groups.

The three subgroups of *Onychostoma* species occupy restricted areas; the moderate-mouth (the mouth width spans that of the head) group is confined to the north of the Nanling Mountain Range; the narrow-mouth group to the west of south China and the wide-mouth group to the east of south China. A half of the species of *Onychostoma* are found in the Pearl River system, which suggests that Pearl River system has been the evolutionary centre of *Onychostoma*.

As yet the relationships of the *Onychostoma-Cyprinion* group to other cyprinines remains unresolved.

ACKNOWLEDGEMENTS. I am most grateful to the staff of the Fish Section of the British Museum (Natural History) for their help. Particular thanks are due to Gordon Howes for his correction of the manuscript and for his many helpful suggestions that have aided my research. I am indebted to Alwyne Wheeler for his help in arranging my work in the Museum, and to James Chambers for his assistance on preparing alizarin specimens.

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Manuscript accepted for publication 14 September 1988

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Bulletin British Museum (Natural History)
ZOOLOGY SERIES
Vol. 55, No. 1, May 1989

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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

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ISBN 0 565 05046 X
ISSN 0007 – 1498

Zoology Series
Vol 55 No 2 pp 123 – 257

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 26 October 1989

Typeset by J & L Composition, Filey, North Yorkshire
Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

Bull. Br. Mus. nat. Hist. (Zool) **55**(2): 123–171 Issued 26 October 1989

Studies on the Deep Sea Protobranchia: The Subfamily Ledellinae (Nuculanidae)

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SYNOPSIS Fourteen species of *Ledella* occurring in the Atlantic are described, five of which are new species, namely, *L. jamesi*, *L. lusitanensis*, *L. sandersi*, *L. similis* and *L. verdiensis*.

Species of the subfamily Ledellinae are usually small, less than 7 mm total length, with shells that are solid, concentrically ridged, ovate, medially or submedially rostrate, and with an amphidetic predominantly internal ligament.

The morphology of *Ledella* is very conservative, the only organ that shows any marked variation in form is the hind gut. Five different configurations of the hindgut occur and these can be derived by radiate or sequential evolution from the primitive condition in which the hind gut forms a single deep loop on the right side of the body.

Although the three most widely distributed species are confined to abyssal depths, endemic species also occur at abyssal depths in individual basins.

The most common species, *L.ultima*, is distributed throughout the Atlantic over a wide depth range. Its success can not only be related to the possesion of a greatly extended hindgut, and therefore a more efficient digestive ability, but also to the fact that the oldest specimens show a marked change in the direction in the growth of the shell edge. The effect of this latter is to increase the shell space and providing more for eggs in comparison to those species that do not have this peculiarity of growth. Egg and prodissoconch size indicate that development is lecithotrophic with a short distributional larval phase.

INTRODUCTION

This is the sixth paper in a continuing series devoted to the taxonomy, ecology, functional morphology of the Protobranchia of the deep Atlantic (Allen & Sanders, 1973, 1982; Sanders & Allen, 1973, 1977, 1985).

In this paper we turn to the genus *Ledella* Verrill & Bush, 1897. Here we consider fourteen species and four subspecies. Eight of the species have been previously described. These latter descriptions are mostly concerned with shell features, many of them are inaccurate and incomplete with no, or at most, scanty, detail of the internal morphology. The subfamily Ledellinae was defined in an earlier paper in the series (Allen & Sanders, 1982) and compared with the Spinulinae and this description is also given in an account of the taxonomy of the protobranch bivalves of the world (Allen & Hannah, 1986) and need not be repeated here other than to state that it is a predominantly abyssal group of small, characteristically rostrate, shells, in which the rostrum is medial or submedial and the ligament is internal or predominantly so. Although additional genera have been described recently from the Pacific (Filotova & Schileko, 1984), in the Atlantic two genera are recognised, namely *Ledella* (see Warén, 1981) and *Tindariopsis*.

The subfamily is of considerable interest in that within it is exhibited almost the full range of hind gut configurations that occur in the subclass Protobranchia, and thus illustrate the evolutionary pathways by which these configurations have been achieved. The subfamily also contains one of the most common species of protobranch molluscs present in deep water (*L. ultima*), with samples sufficiently large to form some opinion as to its ecology and the reasons for its success. Finally, from the wealth of material at our disposal, this study is able to correct a number of taxonomic discrepancies that have appeared in the past literature.

We would like to thank the following people for their interest, support, discussion and their contribution of material and for many other kindnesses without which this contribution would have been much the poorer.

Dr. H. L. Sanders and Dr. F. Grassle, Woods Hole Oceanographic Institution; Dr. A. Warén, Swedish Museum of National History, Stockholm; Dr. Jorgen Knudsen, University of Copenhagen; M. P. Bouchet, Museum National d'Histoire Naturelle, Paris; M. Segonzac, Centob, Brest; Dr. J. Taylor and the staff of the Mollusca Section of the British Museum of Natural History. As in the previous papers in this series, we describe one common species in considerable detail and use this description as a basis for comparison with other species and, in descriptions of the latter, only list features that define and differ from those first described.

Abbreviations to text figures

aa:	anterior adductor
ag:	gland aperture
an:	anus
apr:	anterior pedal retractor muscle
as:	anterior sense organ
by:	byssal gland
cg:	cerebral ganglion
cn:	central nerve
co:	viscero-cerebral commissure
dh:	dorsal hood
di:	digestive diverticula
fa:	feeding aperture
fr:	faecal rod
ft:	foot
gc:	gland cells
gi:	gill
gs:	gastric shield
hg:	hind gut
ht:	heart
if:	inner mantle fold
ky:	kidney
li:	ligament
ma:	mantle
mf:	muscle fibres
mfs:	middle mantle fold
mh:	mouth
ni:	nuclei
oe:	oesophagus
of:	outer mantle fold
ov:	ovary
pa:	posterior adductor
pb:	palp proboscis
pe:	periostracum
pg:	pedal ganglia
pp:	palp
ppr:	posterior pedal retractor muscle
rj:	rejection tract
sa:	divided sole of foot
sf:	secondary mantle fold
si:	siphon
sr:	sorting ridges
ss:	style sac
st:	stomach
sy:	statocyst
te:	tentacle
tm:	transverse muscle
ts:	testis
vg:	visceral ganglion

Family **NUCULANIDAE** Adams & Adams 1858

Subfamily ***LEDELLINAE*** Allen & Sanders 1982

Shell robust, elongate, moderately inflated, veneriform or ovate with characteristically short rostrum, rostrum medial or submedial, concentric sculpture, usually marked but occasionally faint, in some species incomplete radial striae present; umbo approximately central; posterior dorsal margin convex, ventral margin of older specimens characteristically broad and flat, postero-ventral margin sinuous to a greater or lesser degree; hinge plate well developed, hinge teeth stout chevron-shaped; ligament internal and/or external; hindgut with various configurations; adductor muscles approximately equal in size; siphons combined, but usually form a single lumen, palps with relatively few ridges.

Ledella Verrill & Bush 1897

TYPE SPECIES. *Leda ultima* Smith 1885; by subsequent designation.

[*nom. sub. pro Ledella messanensis* (Seguenza MS); Verrill & Bush, 1897, (non Seguenza MS *in* Jeffreys, 1870) = *Ledella bushae* Warén, 1978 (ICZN, 1985. Opinion 1306); herein, (ICZN 1985. Art. 78 F (iv).]

TYPE LOCALITY. Challenger Sta. 5, 24° 28′W, 5011 m. southwest of the Canary Islands.

SYNONOMY. *Junonia* Seguenza, 1877 (non Hübuer, 1818); *Comitileda*, Iredale, 1924; *Magaleda*, Iredale, 1919.

Shell small, short, robust, surface matt, concentric sculpture with scattered incomplete, radial striae in some species, well defined rostrum, usually unicarinate at margin of escutcheon; ventral margin broadly flattened in older specimens of some species, postero-ventral margin sinuous; anterior and posterior hinge teeth series separated by amphidetic, internal ligament, central apex of outer layer of ligament visible externally; hind gut loops in various configurations.

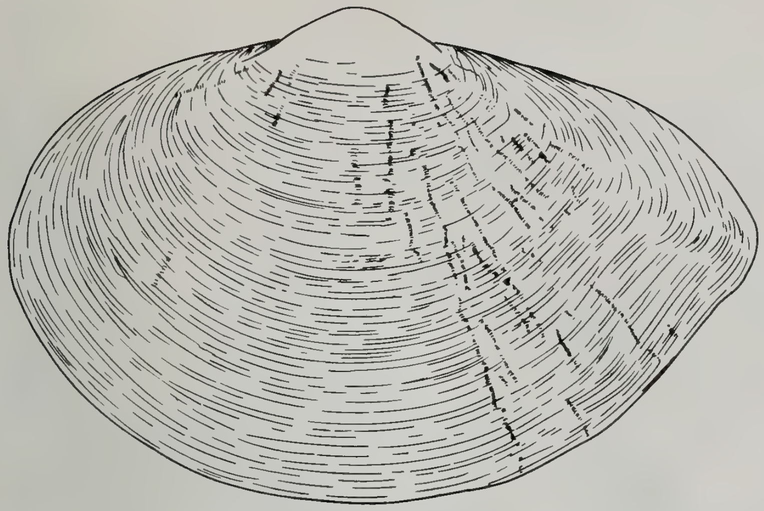

Fig. 1 *Ledella pustulosa pustulosa*: Shell drawn to show lateral view of left valve of a specimen from Biscay. (Sta. Biogas I, DS11). (Scale = 1 mm).

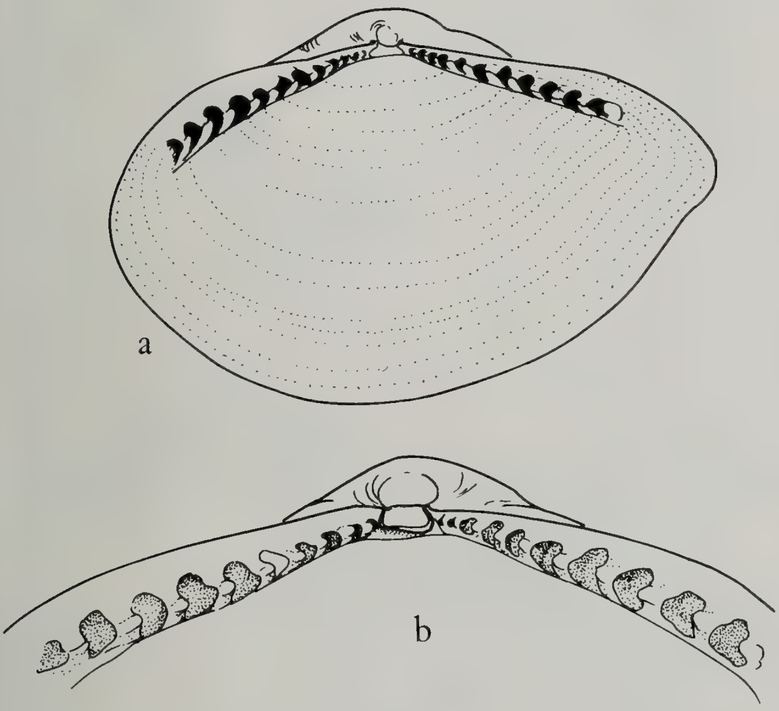

Fig. 2 *L. pustulosa pustulosa*: a) Internal view of right valve of a specimen from Biscay. (Sta. Biogas IV. CP01); b) Detail of hinge plate of left valve of the lectotype (BMNH No. 85.11.5.482). (Scale = 1 mm).

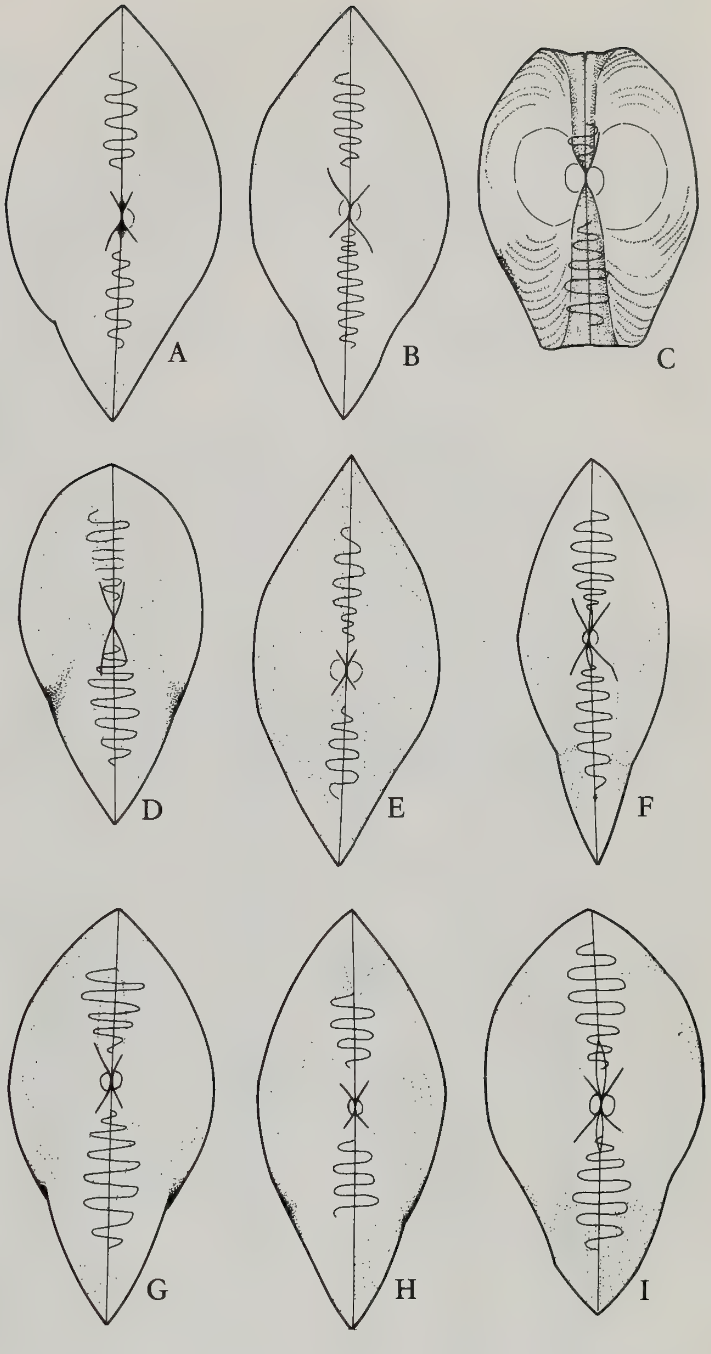

Fig. 3 Dorsal views of the shells of various species of *Ledella* for comparison. *A, Ledella pustulosa marshalli*; B, *L. pustulosa pustulosa*; C, *L. ultima*; D, *L. lustanensis*; E, *L. pustulosa argentinae*; F, *L. acuminata*; G, *L. sublevis*; H, *L. jamesi*; I, *L. solidula*.

Ledella pustulosa pustulosa (Jeffreys, 1876)

LECTOTYPE. British Museum (Natural History) BM(NH) 18 85.11.5.482.

TYPE LOCALITY. Porcupine Expedition (1869) Station 23a, West of Ireland, 768 m.

Because at least six species are included in the previously identified collections of this species that are present in the U.S. National Museum (USNM) (see below) we have assigned a lectotype from the material present in the British Museum of Natural History (BMNH). From an extensive synonymy only those listed below can be ascribed to *L.p. pustulosa* with certainty.

SYNONYMY. *Leda pustulosa* Jeffreys, 1876. *Ann. Mag. Nat. Hist.* Ser. 4, *18*, p. 430 (in part).
Leda (Junonia) pustulosa Jeffreys: Seguenza, 1877. *Atti Reale Accad. Lincei Mem.* Ser. 3, *1*, p. 1177, pl. 3, fig. 17.
Leda pustulosa Jeffreys: Jeffreys, 1879. *Proc. Zool. Soc. Lond.* 1879. p. 576 (in part).
Nuculana pustulosa (Jeffreys): Smith, 1889. *Ann. Mag. Nat. Hist.* Ser. 4, *6*, p. 425.
Leda pustulosa Jeffreys: Locard, 1898. *Exp. Sci. Traveilleur Talisman*. p. 345.
Leda pustulosa Jeffreys: Friele & Grieg, 1901. *Norw. N. Atl. Exped. 6*, p. 28.

MATERIAL. The following specimens labelled *L. pustulosa* in the collections of the USNM & BMNH were examined.
USNM No. 199581 Porcupine 1869 st. 16, 1492 m in part (2 other species present)
USNM No. 199575 Porcupine 1869 st. 23, 1214 m
USNM No. 199576 Porcupine 1869 st. 28, 2222 m.
BM(NH) No. 1885.11.5.387–9 Porcupine 1869 st. 28, 2222 m.

USNM No. 199579 Porcupine 1869 st. 58, 987 m.
USNM No. 199580 Porcupine 1869 st. 2, 557 m.
USNM No. 199586 Travailleur st. 3,1262m. ?(Museum label does not match station list on Locard text)
USNM No. 199582 Porcupine 1870 st. 17a, 1353 m*
USNM No. 199583 Porcupine 1870 st. 17a, 1353 m.*
USNM No. 199584 ? Origin, in part (1 other species present)
**L. p.hampsoni* (see p. 138)

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			WEST EUROPEAN BASIN				
La Perle	DS06	2090	2	47°30.5′N	8°18.5′W	DS	6. 8.72
(Biogas I)	DS07	2170	5	47°30.5′N	8°15.5′W	DS	6. 8.72
	DS09	2130	4	47°30.2′N	8°16.0′W	DS	7. 8.72
	DS11	2205	11	47°35.5′N	8°33.7′W	DS	8. 8.72
	DS12	2180	4	47°28.5′N	8°35.5′W	DS	9. 8.72
	DS13	2165	12	47°33.7′N	8°39.9′W	DS	9. 8.72
Jean Charcot	DS32	2138	56	47°32.2′N	8°05.3′W	DS	19. 4.73
(Biogas II)							
(Biogas III)	DS35	2226	8	47°34.4′N	8°40.7′W	DS	24. 8.73
	DS36	2147	7+2V	47°32.7′N	8°36.5′W	DS	24. 8.73
	DS37	2110	19	47°31.8′N	8°34.6′W	DS	24. 8.73
	DS38	2138	26	47°32.5′N	8°35.8′W	DS	25. 8.73
	DS49	1845	13	44°05.9′N	4°15.6′W	DS	1. 9.73
	DS50	2124	15+1V	44°08.9′N	4°15.9′W	DS	1. 9.73
(Biogas IV)	DS51	2430	3+1V	44°11.3′N	4°15.4′W	DS	18. 2.74
	DS52	2006	47	44°06.3′N	4°22.4′W	DS	18. 2.74
	DS62	2175	18	47°32.8′N	8°40.0′W	DS	26. 2.74
	DS63	2126	78	47°32.8′N	8°35.0′W	DS	26. 2.74
	DS64	2156	58	47°29.2′N	3°30.7′W	DS	26. 2.74
	CP01	2245	21	47°34.6′N	8°38.8′W	CP	25. 2.74
	CP02	2177	2	47°33.2′N	8°41.4′W	CP	26. 2.74
	KR39	2179	2	47°33.8′N	8°36.4′W	KR	25. 2.74
Cyros	DS70	2150	1	44°08.8′N	4°17.4′W	DS	21. 6.74
(Biogas V)	CP07	2170	28	44°09.8′N	4°16.4′W	CP	21. 6.74
Jean Charcot	DS71	2194	44	47°34.3′N	8°33.8′W	DS	20.10.74
(Biogas VI)	DS86	1950	76	44°04.8′N	4°18.7′W	DS	31.10.74
	DS87	1913	123	44°05.2′N	4°19.4′W	DS	1.11.74
	DS88	1894	7	44°05.2′N	4°15.7′W	DS	1.11.74
	CP08	2177	16+3V	44°33.2′N	8°38.5′W	CP	20.10.74
	CP09	2171	14+1V	47°33.0′N	8°44.1′W	CP	20.10.74
	CP24	1995	9+5V	44°08.1′N	4°16.2′W	CP	31.10.74
	CP25	1894	6+2V	44°05.0′N	4°17.0′W	CP	1.11.74
Jean Charcot	DS15	2246	4	47°35.2′N	8°40.1′W	DS	21.10.72
(Polygas)	DS18	2138	8	47°32.2′N	8°44.9′W	DS	22.10.72
	DS25	2096	16	44°08.2′N	4°15.7′W	DS	1.11.72
	DS26	2076	57+1V	44°08.2′N	4°15.0′W	DS	1.11.72
	CV10	2108	5	47°30.7′N	8°40.6′W	CV	22.10.72
Thalassa	Z453	1975–2070	5	48°34.0′N	10°51.6′W	CP	28.10.75
Sarsia	44	1739	1	43°40.8′N	3°35.2′W	ED	16. 7.67
	65	1922	31	46°15.0′N	4°50.0′W	ED	25. 7.67
Jean Charcot	DS01	2091	1246	57°59.2′N	10°41.3′W	DS	15. 7.76
(Incal)	KR01	2093	1	57°59.2′N	10°41.3′W	KR	16. 7.76
	DS02	2081	2135	57°58.5′N	10°49.2′W	DS	16. 7.76
	CP01	2068–2040	408	57°56.4′N	10°55.0′W	CP	16. 7.76
	CP02	2091	27	57°57.7′N	10°44.6′W	CP	16. 7.76
	DS03	609–619	3	57°24.8′N	11°04.0′W	DS	17. 7.76
	DS05	2503	3	56°27.6′N	11°12.0′W	DS	18. 7.76
	CP08	2644	1	50°15.2′N	13°14.8′W	CP	17. 7.76
	CP09	2659	2	50°14.3′N	13°16.1′W	CP	27. 7.76
	OS01	2634	1	50°15.2′N	13°11.0′W	OS	30. 7.76
	WS01	2550–2539	4	50°19.3′N	13°06.9′W	WS	30. 7.76
	WS02	2498–2505	25	50°20.0′N	12°56.0′W	WS	30. 7.76
Chain 106	313	1500–1491	456	51°32.2′N	12°35.9′W	ES	17. 8.72
	314	1006–1015	1	51°54.7′N –50°58.7′N	12°27.3′W 13°01.6′W	ES	18. 8.72
	316	2173–2209	12	50°57.7′N	13°01.3′W	ES	18. 8.72
	318	2506	6	50°27.3′N –50°26.8′N	13°20.9′W 13°19.9′W	ES	19. 8.72
			CANARIES BASIN				
Discovery	6701	1934	43	27°45.2′N	14°13.0′W	ED	16. 3.68
	6704	2129	6	27°44.9′N	14°25.0′W	ED	17. 3.68

This is one of four closely related subspecies described here.

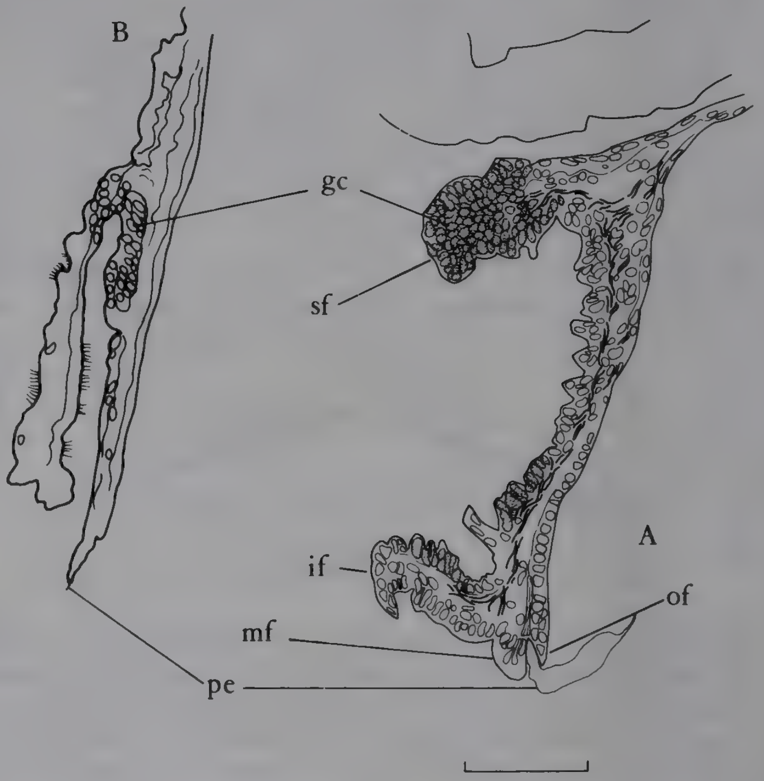

Fig. 4 *L. pustulosa pustulosa*: (A) Transverse section of mantle edge through region of posterior feeding aperture; (B) Transverse section through the anterior sense organ of the mantle. (Scale = 0.05 mm).

DESCRIPTION (Figs 1, 2, & 3). Shell ovate, rostrate, moderately thin, often somewhat transparent, moderately inflated; periostracum straw coloured, preserved specimens may appear 'blistered' giving a tortoise-shell effect, slightly iridescent; sculpture, fine concentric ridges, distance between ridges variable, ridges intersected by radial striae from umbo to ventral margin; radial markings vary from faint to conspicuous, may be obvious across whole shell but usually most obvious around umbo and close to sinuosity, in some striae only observed with difficulty; dorsal margin weakly convex, antero-dorsal margin gradually inclined to anterior limit of hinge plate, then slopes rapidly to form curve of anterior margin, postero-dorsal margin gradually slopes to posterior limit of hinge plate, then forms posterior dorsal margin of short rostrum, posterior ventral margin sinuous, ventral margin long, moderately convex, smoothly curved; umbo approximately equilateral or very slightly displaced posteriorly (average umbo to posterior margin length/total length = 0.48), umbo moderately inflated and posteriorly directed, keel extends from umbo to tip of rostrum, concentric ridges form acute angle at keel; hinge plate moderately strong, long, fairly narrow, 6–12 anterior and posterior chevron-shaped teeth (number depending on size), distal teeth strong, proximal teeth becoming progressively smaller, innermost difficult

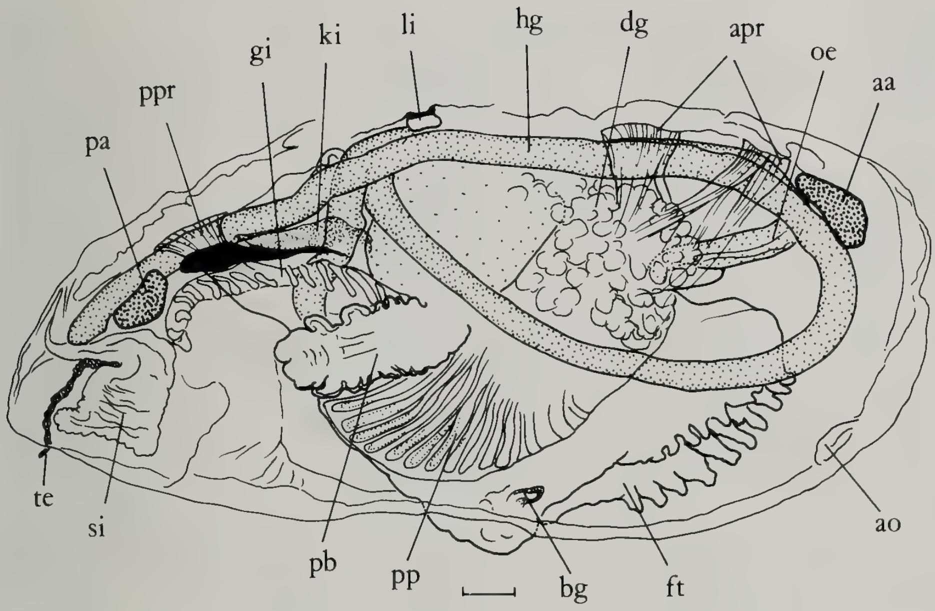

Fig. 5 *L. pustulosa pustulosa*: Lateral view of specimen from right side with shell removed to show the arrangement of the body organs. Note only the section of hind gut to the right side of the body is shown. (Scale = 0.1 mm).

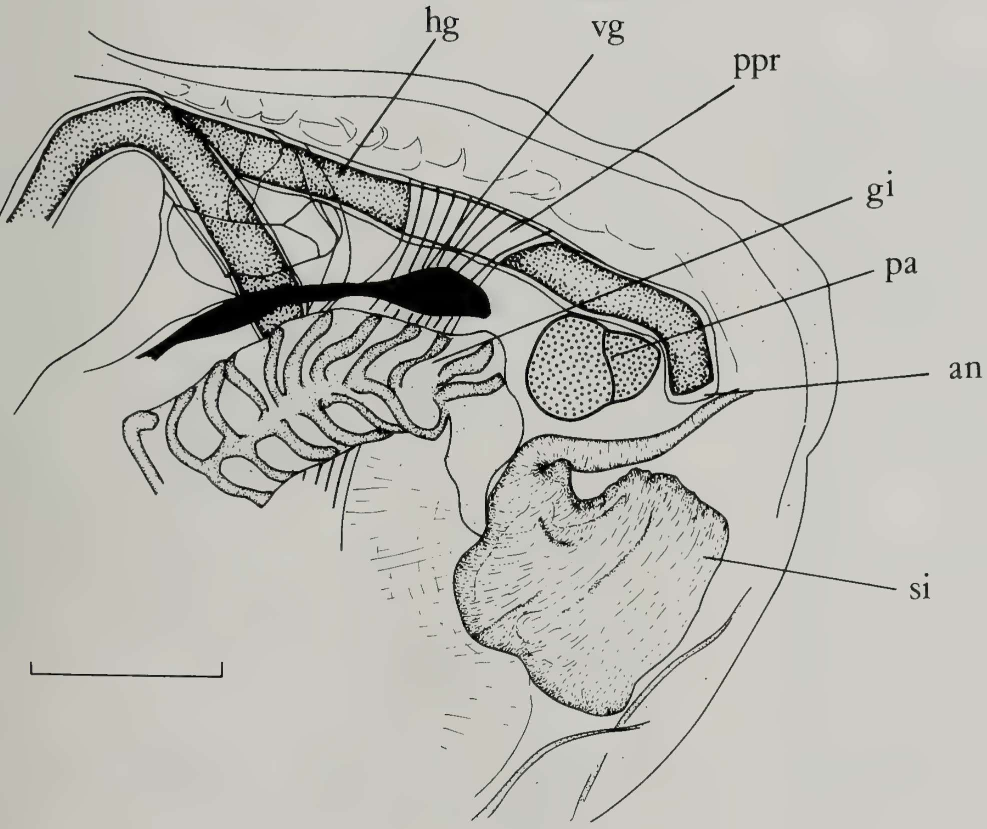

Fig. 6 *L. pustulosa pustulosa*: Detail from lateral view from left side to show detail of siphon and associated organs. (Scale = 0.1 mm).

to discern; ligament amphidetic, internal; resilium, trapezoidal to triangular in shape, moderately large.

Larval shell length 250µm; maximum recorded length 5.61 mm.

MORPHOLOGY. The mantle margin is for the most part unfused and is of the basic bivalve form with three folds. The middle sensory fold is moderately extended as a flap. The inner muscular fold is not greatly thickened, being little thicker than the general mantle epithelium, but is relatively broad. Few gland cells are present in the mantle margin. Posteriorly the mantle forms a siphon combining inhalent and exhalent parts. The combined siphon is a laterally compressed tube, which in preserved specimens, is completely retracted in an S-shape within the shell (Figs. 5 & 6). It is probable that the siphon is extended from a position just below the ventral edge of the rostrum. The siphon is muscular with relatively thick inner and outer epithelial columnar cells.

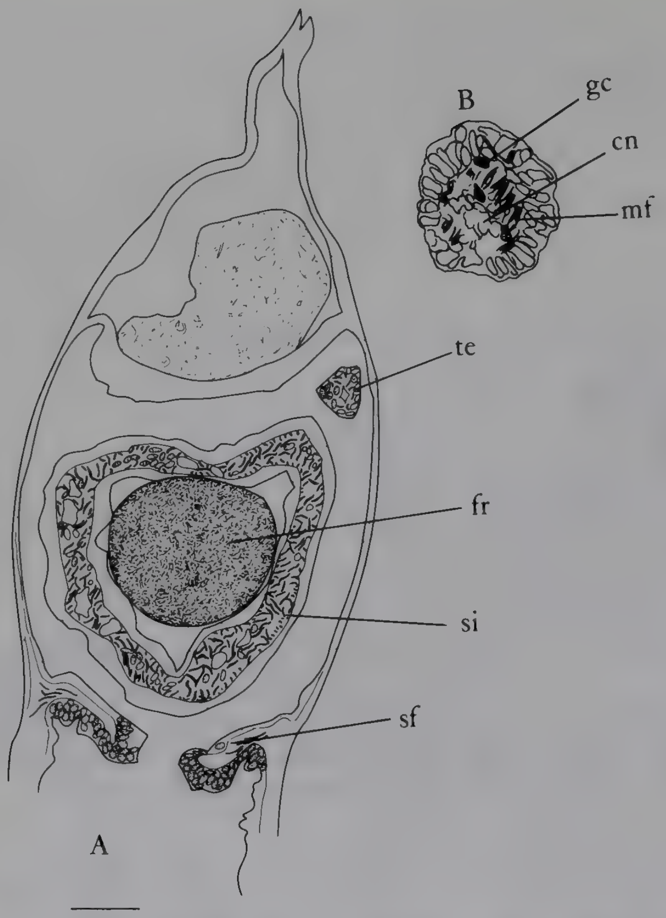

Fig. 7 *L. pustulosa pustulosa*: a) Transverse section through the combined siphon; b) Transverse section through the siphonal tentacle. (Scale = 0.1 mm).

A narrow band of longitudinal muscle fibres lie immediately internal to the basal membrane of the outer epithelium. Internal to the longitudinal layer, the muscles consist of short circular fibres with the occasional transverse fibre between inner and outer basal membranes. Scattered throughout muscle layer are subepithelial gland cells (Fig. 7a). Although considerably contracted and difficult to discern, there is some evidence to suggest that longitudinal muscle blocks are separated by haemocoelic channels. The faecal rod takes up all of the contracted siphonal space (Fig. 7a). We have no evidence of a functional separation formed by a pair of opposing mid-lateral ridges into upper exhalent and a lower inhalent parts as occurs in some protobranchs. The gill axes posteriorly join with the midlateral section of the siphons (Fig. 6) and the posterior gill plates possibly act to channel the faeces into the siphon. The anus lies close to the anterior limit of the siphon.

The siphonal tentacle, derived from the middle sensory fold of the mantle, is a fine thread-like structure that tapers to a point. It originates from a pocket in the right ventral side of the siphonal embayment. In transverse section, it comprises a large central nerve surrounded by fine muscle fibres interspersed with gland cells and connective tissue covered by an outer layer of glandular epithelial cells (Fig. 7b).

A specialized region of the mantle, the feeding aperture, lies ventral to the siphon. Here the inner muscular mantle fold is greatly extended, a secondary fold is also present that forms an arch defining the internal margin of the feeding aperture (Figs. 4a & 7a). A large concentration of acidophilic gland cells are found on this innermost fold, while others are scattered in the epithelium between the two folds and on the dorsal surface of the inner muscular fold proper. The anterior sense organ is a thickened region of the mantle edge directly below the anterior adductor muscle and is similar to that described for *Spinula subexcisa* (Allen & Sanders, 1982). The adductor muscles are approximately equal in size and oval or somewhat crescent-shaped with obvious 'quick' and 'catch' parts.

The gills lie parallel to the posterior dorsal shell margin and are relatively well developed. The number of plates is related to the size of the individual and the maximum number observed in each demibranch was sixteen. The labial palps are moderately large, with 16–23 ridges according to the size of the animal, with large, broad, palp proboscides. The palps extend approximately three quarters across the body; the mouth opens a short distance posterior to the anterior adductor muscle.

The foot is well developed with a relatively narrow neck (Fig. 8b); the divided sole is elongate with a moderately fine papilliate edge. A 'byssal' gland is present, large enough to be obvious as a bulge in the heel of the foot. The gland is spherical and opens medially at the posterior limit of the divided sole (Fig. 8a). The gland is separated from a section of the hind gut above by a layer of transverse muscle fibres. It is encased by peripheral muscles, a few fibres from which possibly form a sphincter at the neck of the gland. The gland itself is composed of large hyaline cells.

The posterior pedal retractor muscles form a thick wide strap which is attached to the shell on either side of the hind gut, just anterior to the posterior adductor muscle. A small postero-lateral pedal retractor muscle is present immediately posterior to the stomach. Three pairs of anterior pedal retractor muscles are attached to the dorsal margin of the shell between the oesophagus and the anterior part of the hind gut. Muscle fibres to the palp proboscides form part of the most anterior of the two sets of anterior muscles (Fig. 5). In section, muscle fibres from the posterior pedal retractor and the innermost anterior pedal retractor cross below the stomach in the neck region of the foot and attach to opposite walls of the foot thus cradling the stomach (Fig. 10b). These muscles may be important in the mixing and movement of the stomach and gut contents. The musculature of the foot itself consists of an outer layer of circular muscles which appear to originate from the posterior pedal retractor and an inner longitudinal layer, anterior in origin.

Conspicuous elongate cerebral and visceral ganglia lie internal to the anterior and posterior adductor muscles repectively. The pedal ganglia are large (Fig. 8b), although not always easily detected in whole mounts, they lie immediately below the most ventral section of the hind gut loop. A large statocyst is associated with each pedal ganglion and lies dorsal to it. The statocyst contains numerous small refractile crystals.

From the mouth the ciliated oesophagus first curves anteriorly to the posterior face of the anterior muscle then follows a course parallel to the dorsal edge of the shell to enter the stomach high on the left anterior face (Fig. 10b). The stomach, with the style sac, takes up a considerable part of the body space. It is dark brown in colour and lies below the resilium. The style sac penetrates approximately half the length of the foot. A large gastric shield occupies more than a third of the stomach wall and is predominately dorsal in position and extends somewhat to the left (Fig. 9). Posteriorly at the junction of style sac and stomach the shield forms a thick chitinous girdle.

That part of the stomach not covered by gastric shield is

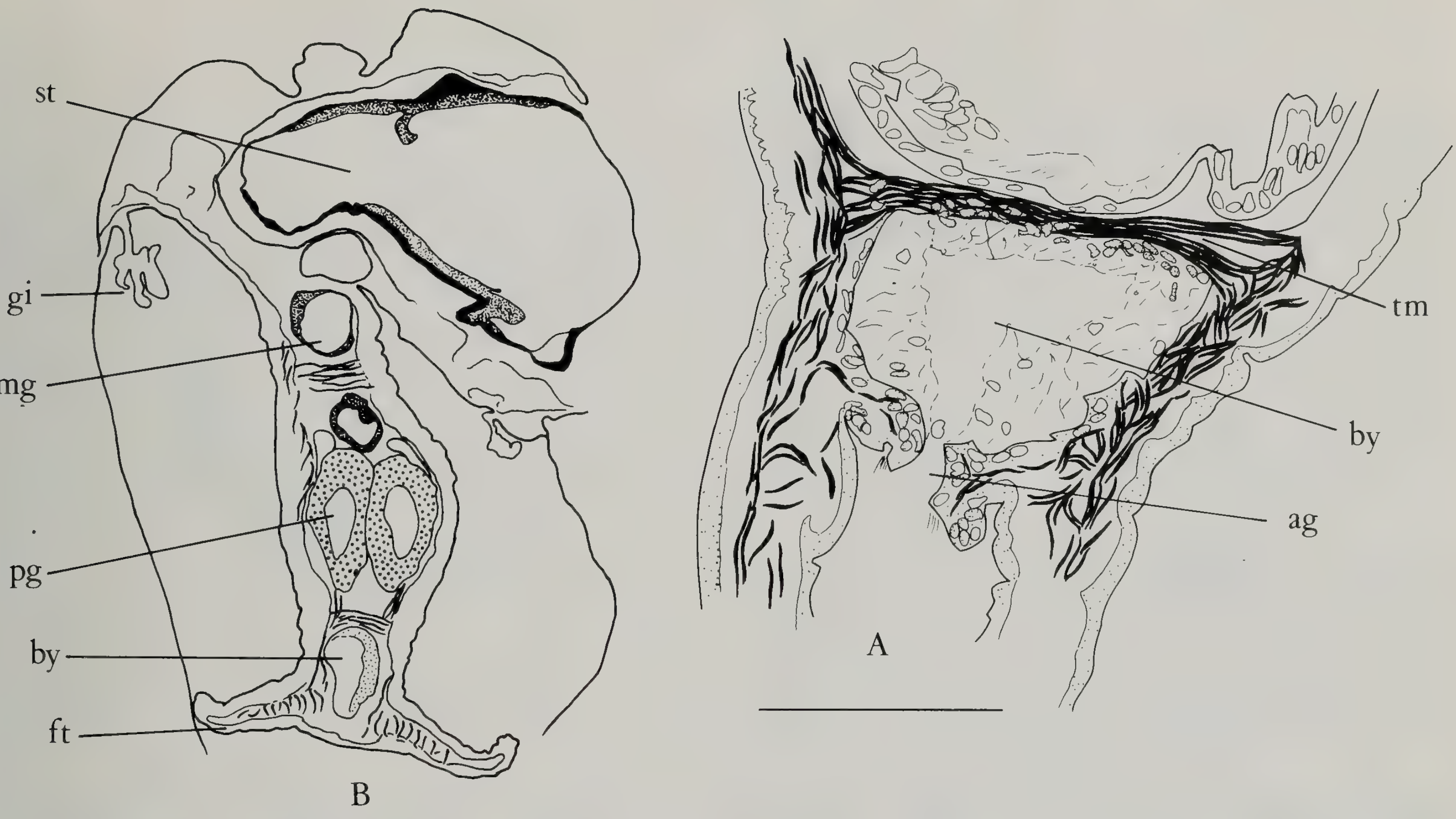

Fig. 8 *L. pustulosa pustulosa*: (a) Vertical transverse section through the 'byssal' gland; (b) Vertical transverse section through the stomach and pedal ganglia. (Scale = 0.1 mm).

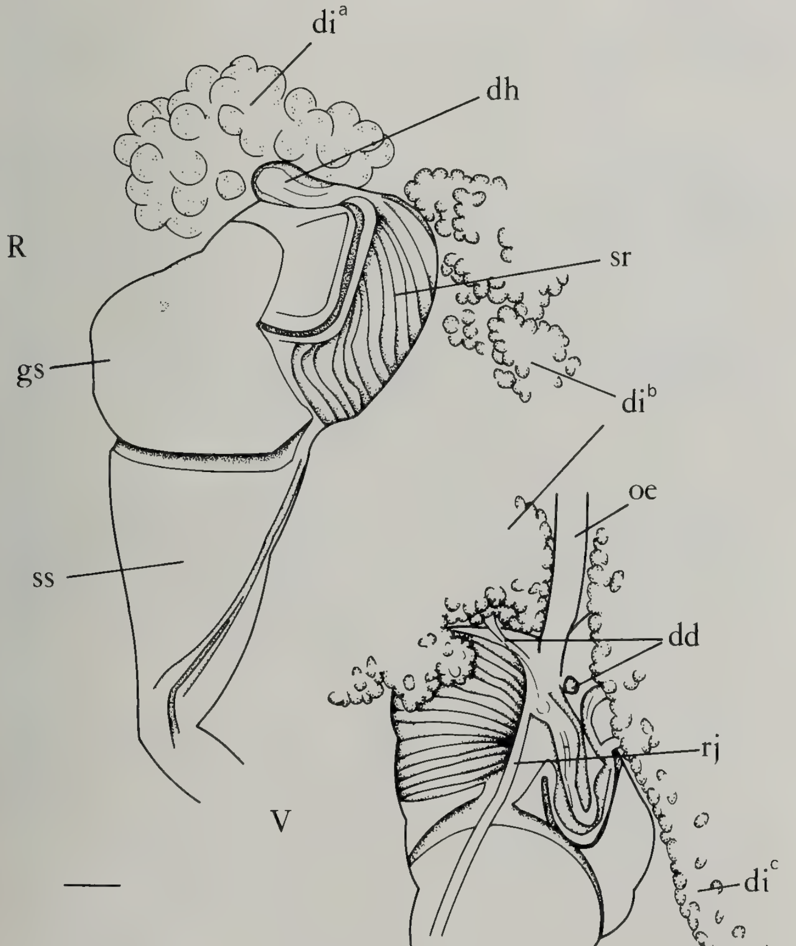

Fig. 9 *Nuculana minuta*: Right lateral (R) and ventral (V) views of the stomach and style sac. (Scale = 0.1 mm).

similar to that described by Yonge (1939) for *Malletia obtusata* and by Purchon (1956) for *Nuculana minuta* (Fig. 9) with the modification that in this deep water species there is a reduction in the number of sorting ridges from fourteen or more to eight. These make up the ciliated portion and form a band of broad ridges, the posterior sorting area that extends across the right side of the stomach (Figs. 9 & 10a) close to the margin of the gastric shield to a line that runs from the lateral margin of the oesophagus, close to an isolated right duct, to the rim of the style sac. At the antero-ventral margin of the posterior sorting area a main rejection tract leads to the midgut. The latter is not separate from the style sac but is guarded from it by major and minor typhlosoles. The major typhlosole extends across the wall of the stomach on the left side to a point below the level of the dorsal hood where it forms a loop close to the apertures of the digestive ducts. It defines a small area referred to by Purchon (1956) as the folded area. It is difficult to be sure in this small species whether this area has transverse folds as those described in *N. minuta*.

The digestive diverticula for the most part cover the anterior wall of the stomach with some posterior extension on either side. They are packed loosely together with little connective tissue between them. One diverticulum lies to the right anterior side and opens to the stomach immediately ventral and to the right of the oesophageal opening. The other two diverticula are situated on the anterior left; one of these opens in the centre of the anterior wall while the other opens more posteriorly and more dorsal to it (Fig. 10a). Externally the appearance of the tubules of this latter diverticulum differ from those of the other two in that their external diameter is larger and that they are paler in colour with a characteristic speckled appearance. The aperture to

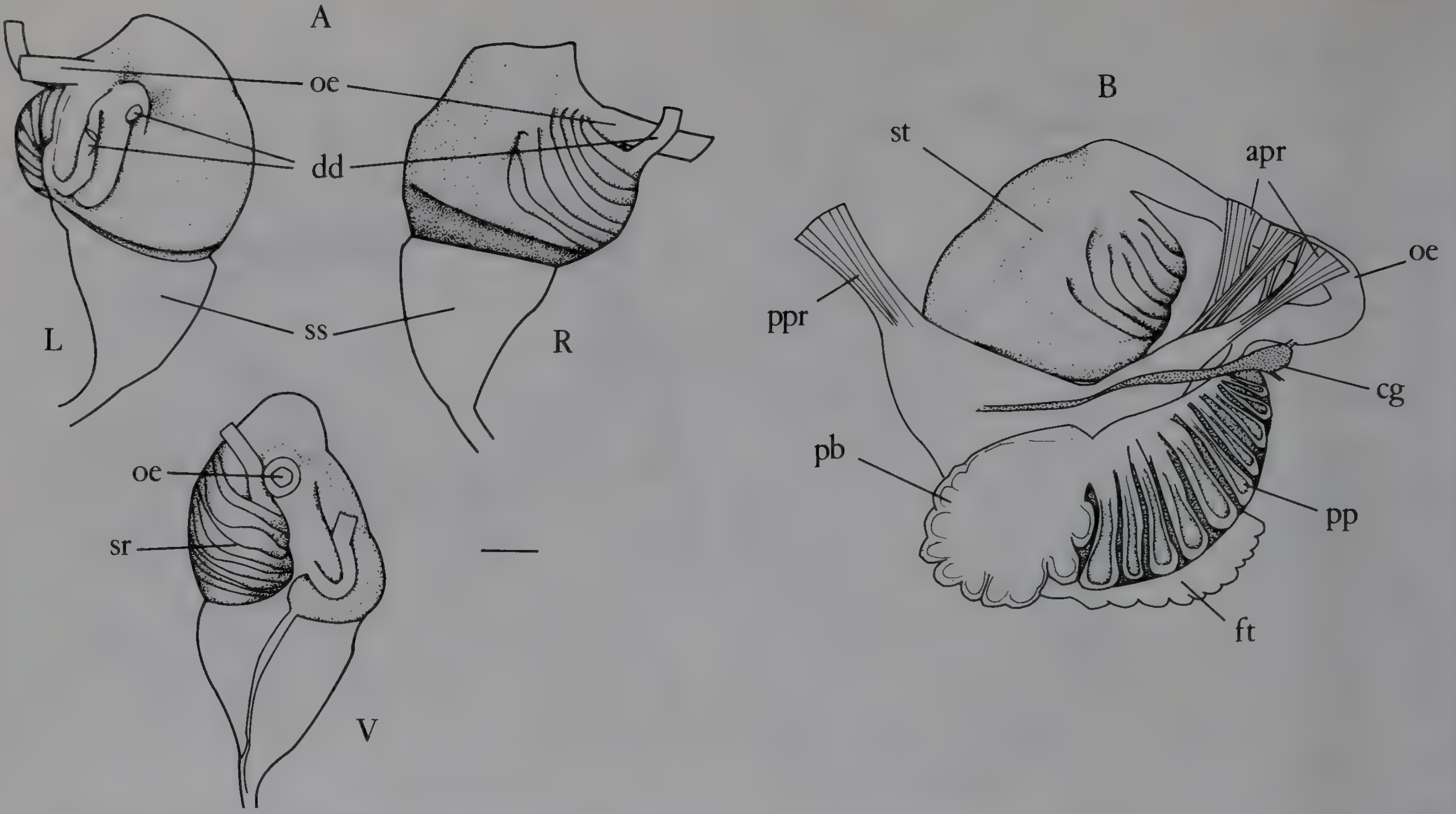

Fig. 10 *L. pustulosa pustulosa*: a) Right (R) left (L) lateral and ventral (V) views of the stomach and style sac, b) lateral view of body, foot and palp from right side. (Scale = 0.1 mm).

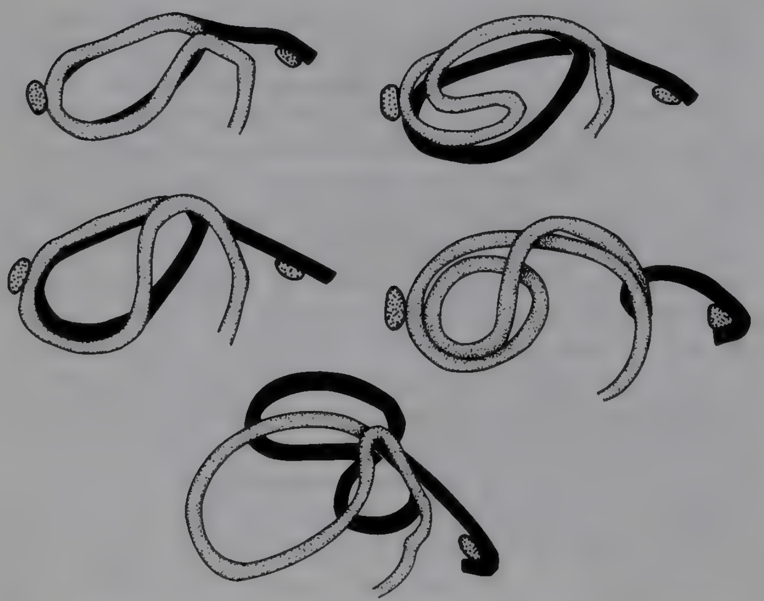

Fig. 11 *L. pustulosa pustulosa*: Variation in the course of the hind gut as seen from the left side. Stippled sections are to the left of the body, black sections to the right of the body. Anterior and posterior adductor muscles are indicated.

this posterior dorsal diverticulum opens almost directly to the tubule system, the digestive duct being reduced to a small collar approximately 10 cells deep close to the aperture. Although it appears that the ducts of the other two diverticula are more extended, sections show that what appears to be duct is formed by vacuolated tubule cells. Little material was observed in the lumen of the digestive gland and, when present, it was only in the upper part of the left hand diverticulum.

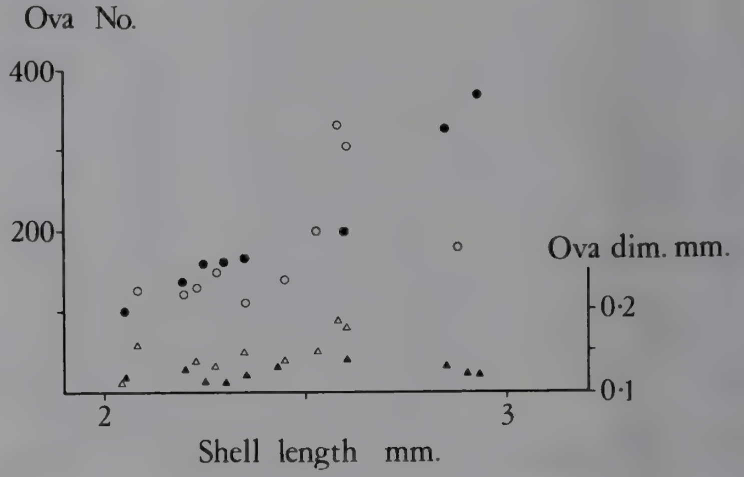

Fig. 12 *L. pustulosa pustulosa*: Ovary development in specimens sampled at different times of the year from similar depths and geographical position. Circles: number of ova; triangles: maximum dimension of ova; open symbols: Biogas III, DS38 (August); closed symbols: Biogas II, DS32 (April).

From the style sac the hind gut extends into the foot first curving anteriorly and ventrally to the pedal ganglion before reversing its course posteriorly and then dorsally behind the stomach. Close to the dorsal margin and immediately posterior to the resilium the hind gut passes to the left side of the body where it forms an anterior loop which curves first ventrally to the anterior adductor muscle and then dorsally and posteriorly to cross to the right of the body anterior to the first crossover point. There it forms a second loop similar to that on the left. Finally, it takes a posterior course close to the dorsal margin passing over the posterior adductor muscle to the anus. An unusual degree of variation in the arrangement of the gut has been observed in this species (Fig. 11). Most of

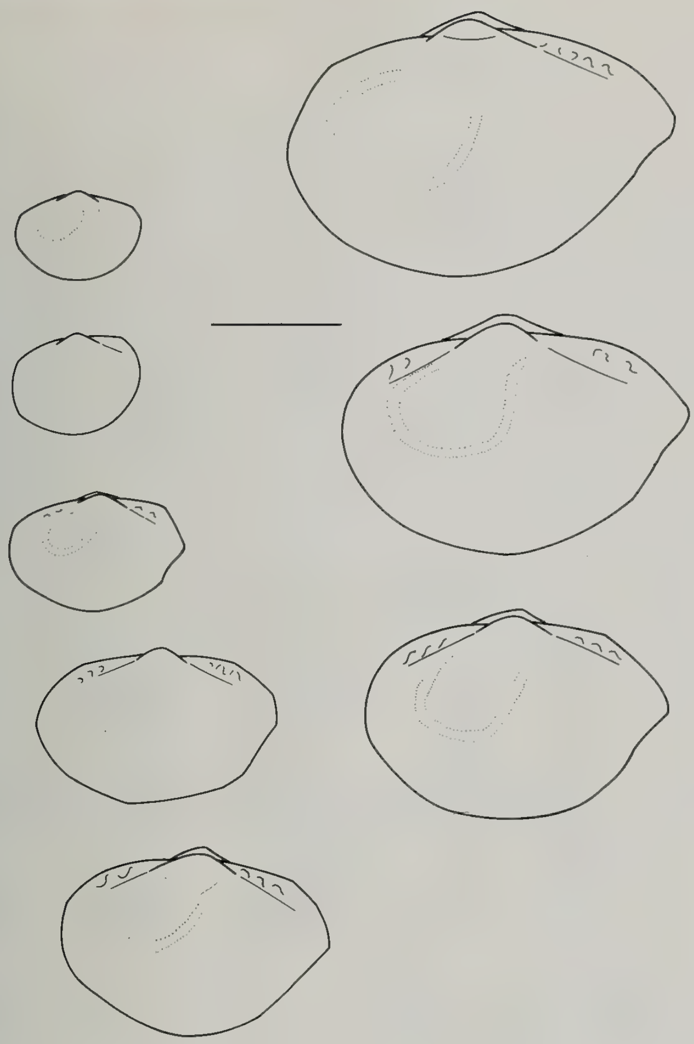

Fig. 13 *L. pustulosa pustulosa*: Growth series of shells in outline seen in right lateral view. (Scale = 1 mm).

these involve one or both of the loops folding back on itself. Sections of the hind gut in the foot show a single typhlosole and although the typhlosole was not obvious in all sections, it could be seen in whole mounts as a ridge running along the complete length of the hind gut. Material in the gut consisted of soft clay with broken skeletal remains. Fragmented diatom and silicoflagellate frustules of several different species were observed. The stomach contents are looser and less compact than the material present in the hind gut.

The sexes are separate. The gonads overlie the lateral and dorsal sides of the hind gut loops and the digestive diverticula. As the gonads develop they first form a ring around the loop of the gut and when mature totally overlie the viscera laterally. The gonadial apertures lie dorsal and close to those of the kidney, immediately anterior to the posterior pedal retractor muscle. No gonad was observed in specimens below 1.6 mm in length but some development had occurred in all specimens above this length (Fig. 16). The ratio of males: females is approximately 1:1. The egg number varies with the size of the individual; approximately 100 eggs were observed in an individual 2.0 mm long while 380 eggs were observed in a specimen of 2.9 mm. Maximum observed length of an egg was 210 μm. Egg numbers and size were compared in two samples taken from a similar area and depth but four months apart (Table, Fig. 12). These perhaps indicate increasing maturity in the four months that separate the samples. The kidney is moderately large, highly ramified. It lies anterior to the posterior pedal retractor muscle and extends anteriorly on either side of the stomach, tapering towards the lateral pedal retractor muscles. A single layer of cuboid cells lines the kidney walls. A large pericaridial cavity lies dorsal and posterior to the stomach; the hind gut passes through this and the ventricle of the heart.

There is some variation in shell shape but variation of specimens within a population is no less that that between populations. A growth series (Fig. 13) shows that the adult shell becomes slightly more elongate with age and the rostrum becomes more prominent. Height to total length ratios and post-umbonal length to total length ratios (Fig. 14) verify visual observation. The size range of individual samples varies considerably. (Fig. 15) but there appears to be no relationship with increasing depth. This variation is probably related to sporadic settlements and is borne out in that population size frequency histograms show variable numbers of peaks within the size range (Fig. 16). These are not necessarily related to age classes but probably to the survival of particular spatfalls.

L. pustulosa appears to be closely related to *Ledella inopinata* Smith. The latter species has been recorded from the Southwest Pacific, off Australia (Smith 1885), off Celebes (Prashad 1932). However, it differs from the present species in its dentition, and grows to a larger size. The Pliocene fossil material from Southern Italy identified by Seguenza (1877) appears to have a prominant escutcheon and a thicker hinge plate and may be a distinct species (Fig. 17).

DISTRIBUTION. Northeastern Atlantic; Rockall; Bay of Biscay; Southwest of Ireland; Canaries. Lower Slope and Abyssal Rise.

DEPTH RANGE. of 58 samples – 609–2659 m, exceptionally two samples (not listed) appear to have been collected from deeper water—4706 m (Biogas IV CP17) and 4829 m (Incal WS03), but we are inclined to believe that this may have been due to incomplete washing of the sampling gear after earlier samples.

Ledella pustulosa marshalli new subspecies

HOLOTYPE. BM(NH) no. 1885.11.5.411 (Paralectotypes of *L. pustulosa*).

PARATYPE. USNM No. 199578 from same Station.

TYPE LOCALITY. Porcupine Expedition (1869) Station 31, 2487 m northwest of Ireland.

SYNONYMY. *Leda pustulosa* Jeffreys 1876 *Ann. Mag. nat Hist.* Ser. 18, *4*, p. 430 (in part).

Leda pustulosa Jeffreys: Jeffreys 1879 *Proc. Zool. Soc. Lond.* 1879, p. 576 (in part).

MATERIAL

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		WEST EUROPEAN BASIN					
Jean Charcot	DS20	4226	2	47°33.0′N	9°36.7′W	DS	24.10.72
(Polygas)	DS21	4190	1	47°31.5′N	9°40.7′W	DS	24.10.72
	DS28	4413	3	44°23.8′N	4°47.5′W	DS	2.11.72
(Biogas III)	DS41	3548	12	47°28.3′N	9°07.2′W	DS	26. 8.73
(Biogas IV)	DS53	4425	6	44°30.4′N	4°56.3′W	DS	19. 2.74
	DS55	4125	2	47°34.9′N	9°40.9′W	DS	22. 2.74
	DS57	2906	1	47°30.8′N	9°07.6′W	DS	23. 2.74
	DS58	2775	5	47°34.1′N	9°08.2′W	DS	23. 2.74

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
(Biogas V)	DS66	3480	1	47°28.2′N	9°0.00′W	DS	16. 6.74
	DS67	4150	1	47°31.0′N	9°35.0′W	DS	17. 6.74
(Biogas VI)	DS73	2805	1	47°32.1′N	9°06.0′W	DS	21.10.74
	DS74	2777	1	47°33.0′N	9°07.8′W	DS	21.10.74
	DS76	4228	5	47°34.8′N	9°33.3′W	DS	23.10.74
	CP10	2878	4	47°29.6′N	9°04.5′W	CP	21.10.74
	CP13	4134	3	47°34.4′N	9°38.0′W	CP	23.10.74
	CP14	4287	1	47°32.0′N	9°35.9′W	CP	23.10.74
Chain 106	321	2890–2868	74	50°12.3′N −50°08.3′N	13°35.8′W −13°53.7′W	ES	20. 8.72
	323	3356–3338	18	50°08.3′N −50°04.9′N	13°50.9′W −14°23.8′W	ES	21. 8.72
	326	3859	12	50°05.3′N	14°24.8′W	ES	22. 8.72
	330	4632	1	50°43.5′N −50°43.4′N	17°51.7′W −17°52.9′W	ES	24. 8.72
Jean Charcot (INCAL)	CP03	2466	14	56°38.0′N −56°37.3′N	11°06.4′W −11°07.8′W	CP	17. 7.76
	CP04	2483–2513	17	56°33.2′N −56°32.5′N	11°11.3′W −11°12.4′W	CP	17. 7.76
	DS05	2503	92	56°28.1′N −56°27.6′N	11°11.7′W −11°12.0′W	DS	18. 7.76
	DS06	2494	99	56°26.6′N −56°25.9′N	11°10.5′W −11°10.7′W	DS	18. 7.76
	DS07	2884	500	55°00.7′N −55°01.0′N	12°31.0′W −12°32.0′W	DS	19. 7.76
	DS08	2891–2884	57	55°02.0′N −55°01.9′N	12°34.6′W −12°33.4′W	DS	19. 7.76
	CP05	2884	222	55°00.4′N −55°00.9′N	12°29.4′W −12°31.1′W	CP	19. 7.76
	CP06	2888–2893	408	55°02.3′N −55°02.6′N	12°40.3′W −12°41.7′W	CP	19. 7.76
	CP07	2895	657	55°03.4′N −55°04.4′N	12°46.2′W −12°46.7′W	CP	20. 7.76
	DS09	2897	1280	55°07.7′N −55°08.1′N	12°52.6′W −12°53.2′W	DS	20. 7.76
	CP08	2644	6	50°14.7′N −50°15.2′N	13°13.5′W −13°14.8′W	CP	27. 7.76
	CP09	2659–2691	2	50°15.4′N −50°14.3′N	13°15.8′W −13°16.1′W	CP	27. 7.76
	DS10	2719	1	50°12.7′N −50°13.2′N	13°16.6′W −13°16.4′W	DS	27. 7.76
	0S01	2634	4	50°14.4′N −50°15.2′N	13°10.9′W −13°11.0′W	OS	30. 7.76
	0S04	4796	1	46°03.9′N	10°12.8′W −10°11.6′W	OS	5. 8.76
	WS07	4281–4274	4	47°30.6′N −47°31.2′N	9°37.1′W − 9°35.7′W	WS	7. 8.76
	DS14	4254–4248	1	47°32.6′N −47°32.9′N	9°35.7′W − 9°35.1′W	DS	7. 8.76
	0S06	4316–4307	1	46°27.3′N −47°29.9′N	9°36.2′W − 9°36.0′W	OS	9. 8.76
	DS16	4268	4	47°29.8′N −37°30.3′N	9°33.4′W − 9°33.4′W	DS	9. 8.76
	WS09	4277	1	47°28.8′N −47°27.9′N	9°34.0′W − 9°34.0′W	WS	10. 8.76
	WS10	4354	2	47°27.3′N −47°28.2′N	9°39.9′W	WS	11. 8.76
	0S08	4327	11	47°29.8′N −47°29.5′N	9°39.2′W − 9°38.8′W	OS	11. 8.76

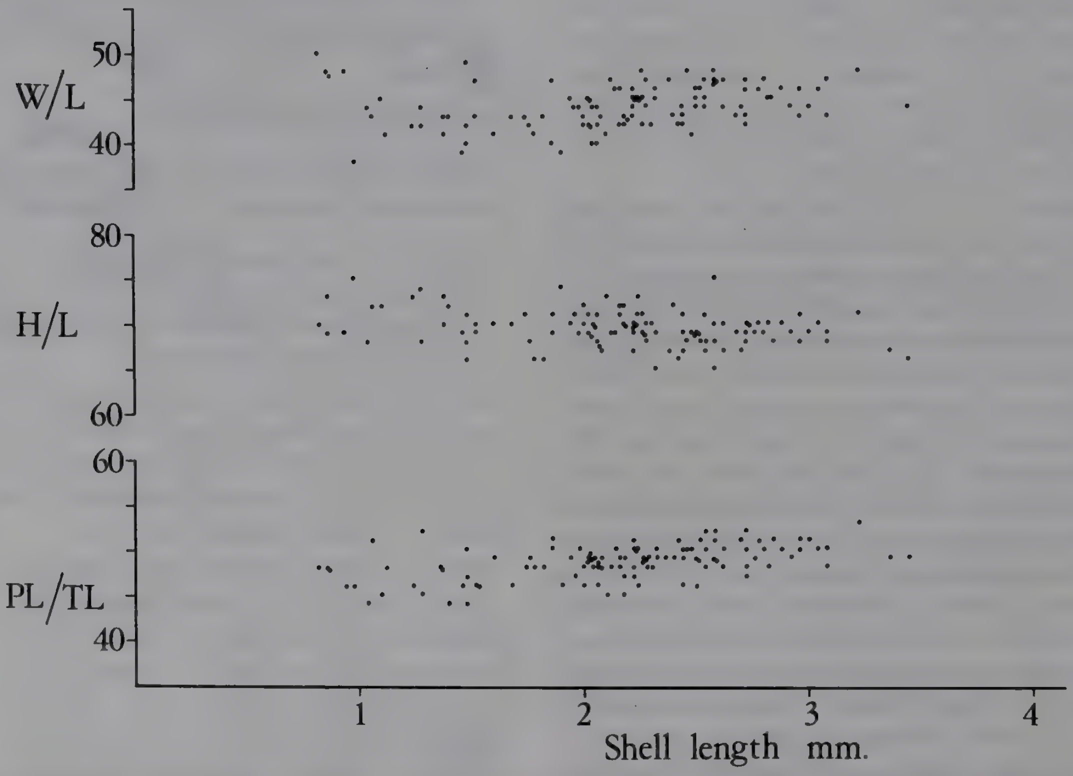

Fig. 14 *L. pustulosa pustulosa*: An analysis of change in shape with growth as shown by the plots, posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) all plotted against length.

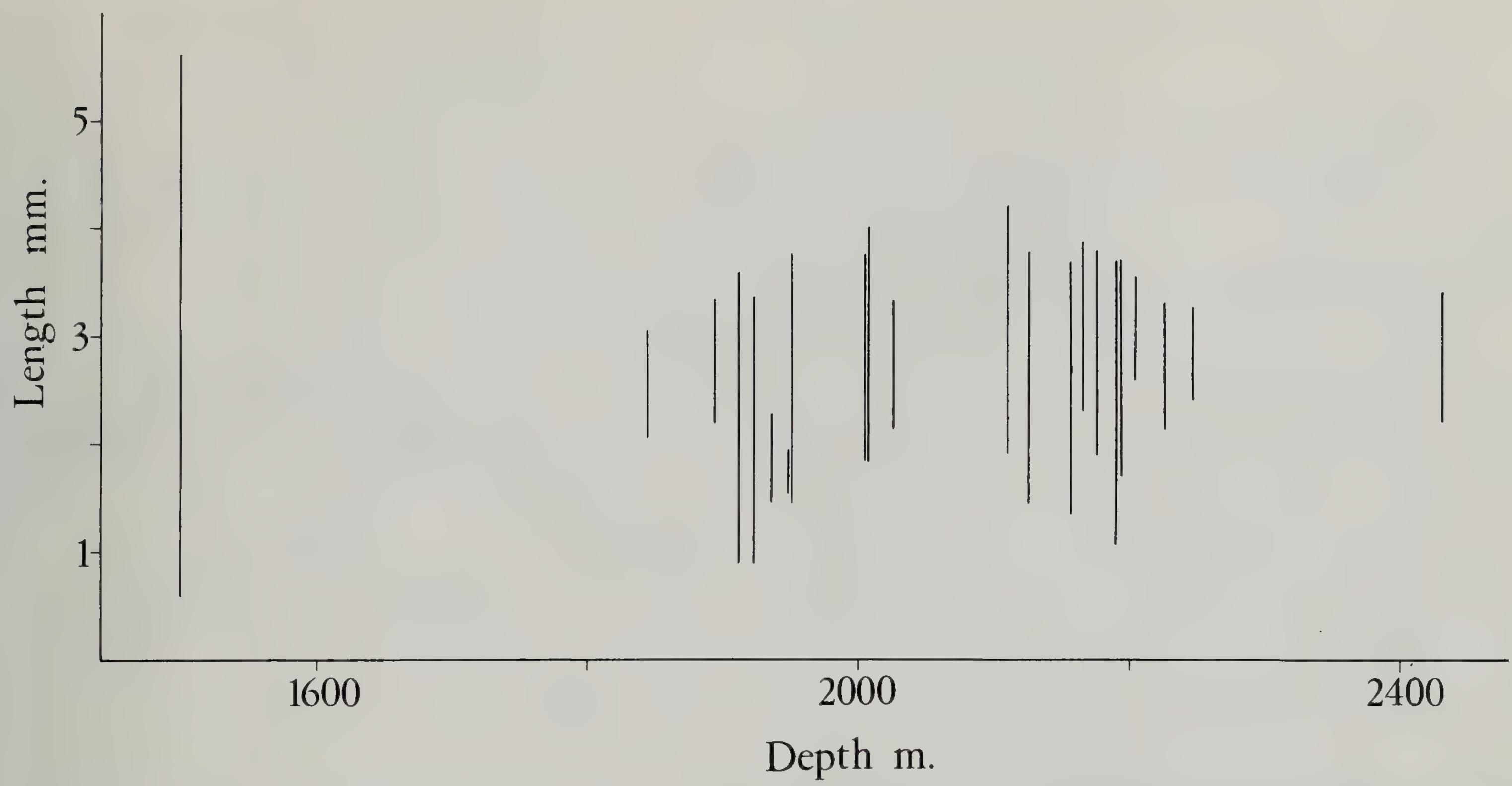

Fig. 15 *L. pustulosa pustulosa*: The range of shell lengths in individual samples taken with an epibenthic sledge plotted against Station depth.

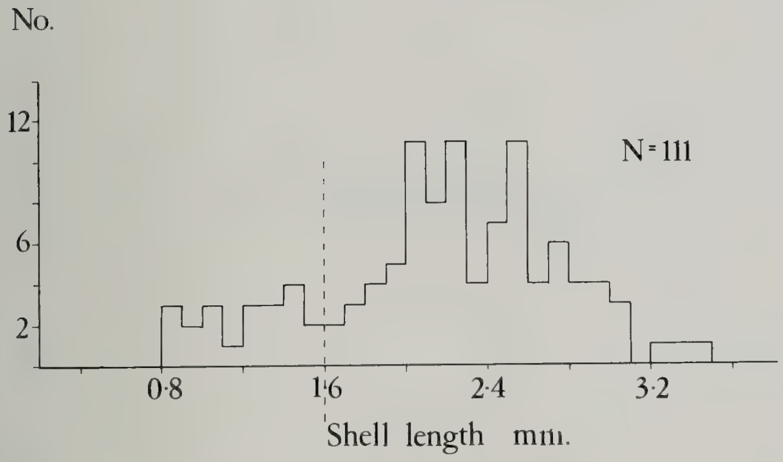

Fig. 16 *L. pustulosa pustulosa*: Length frequency histogram of specimens taken at Station Biogas VI DS87. The dashed line marks the minimum size at which gonadial development was observed.

DESCRIPTION (Figs 18a & b). Shell, similar to *L. p. pustulosa* but differs in being slightly more inflated, the overall lateral outline squarer and more 'angular', anterior and posterior dorsal margin proximally straight, dorsal anterior margin curves sharply into broadly curved anterior margin, posterior dorsal margin continuous curve with dorsal margin of rostrum, tip of rostrum more ventral in position than in *L. p. pustulosa*, posterior ventral margin more deeply sinuous than in *L. p. pustulosa*.

In general *L. p. marshalli* appears to have fewer, broader teeth (range: 5–10 on either side of resilium) than *L. p. pustulosa* (but see p. 125 Fig. 2a)

Larval shell length 245 μm; maximum observed length 5.06 mm.

The internal morphology is virtually undistinguishable from that of *L. p. pustulosa* (Fig. 19). The number of gill filaments and labial palp ridges are of the same order in both subspecies. *L. p. marshalli* possibly has slightly longer gill filaments and larger, broader palp ridges, and the byssal gland appears to be larger. The latter may have some

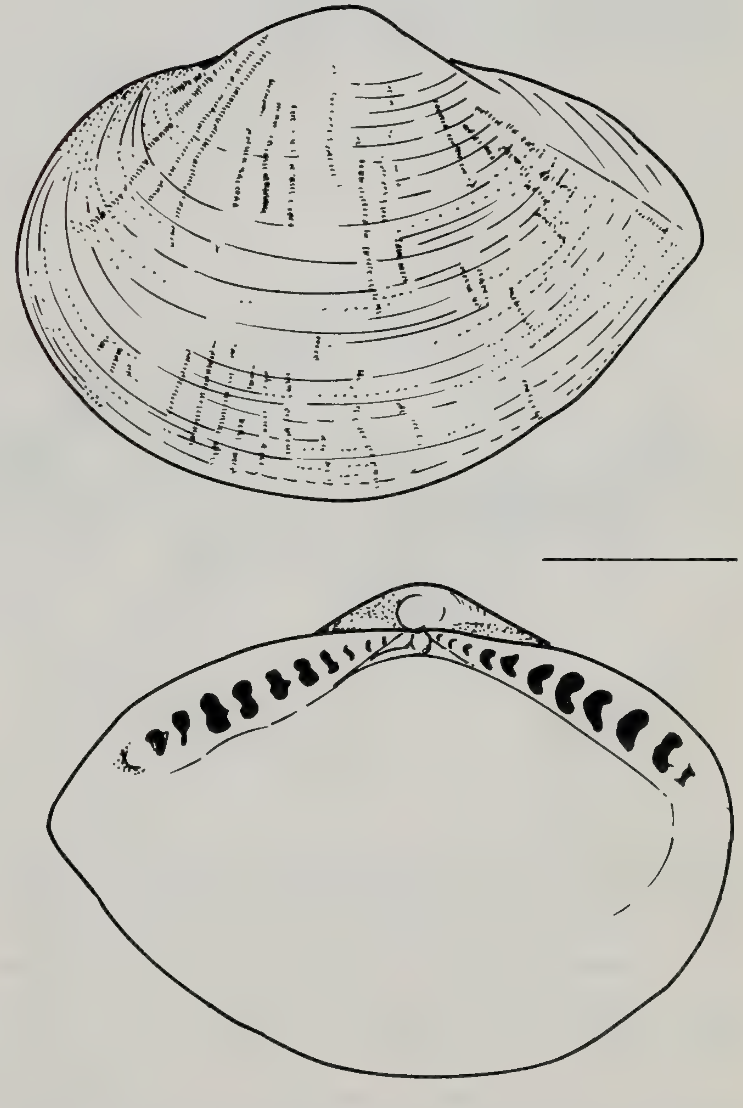

Fig. 17 Specimen No. 199587 from the U.S. National Museum labelled 'Ledella pustulosa (Jeff)', Messina Sicily, Seguenza fossil. (Scale = 1 mm).

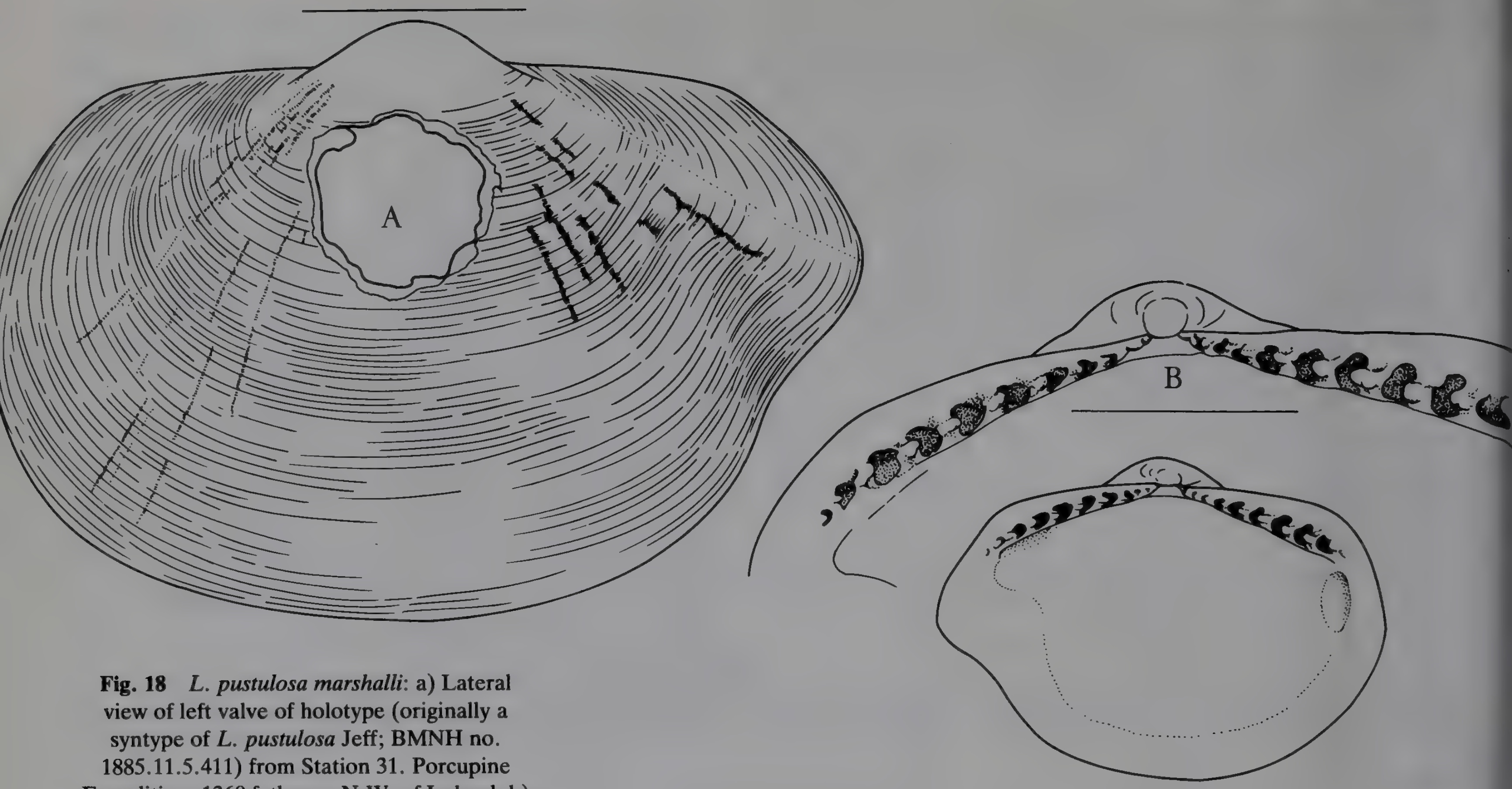

Fig. 18 *L. pustulosa marshalli*: a) Lateral view of left valve of holotype (originally a syntype of *L. pustulosa* Jeff; BMNH no. 1885.11.5.411) from Station 31. Porcupine Expedition, 1360 fathoms, N.W. of Ireland; b) Internal view of same valve with enlarged detail of hinge plate. (Scales = 1 mm).

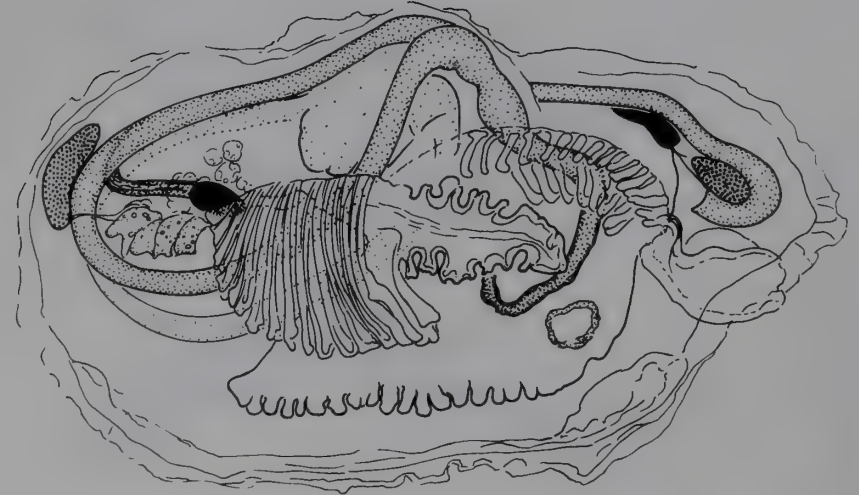

Fig. 19 *L. pustulosa marshalli*: Lateral view of specimen from the left side with shell removed to show arrangement of body organs. (Scale = 1 mm). For identification of parts see Fig. 5.

significance in that generally nuculanoids from deeper depths appear to have larger 'byssal' glands.

Examination of the maturity of individuals of a subsample of *L. p. marshalli* (Incal DS09) shows no gonadial development in specimens below 1.75 mm in length. As in *L. p. pustulosa*, the number of eggs increases with the length of the adult. Thus, there was 59 (maximum egg diameter 120 μm) present in an individual 2.14 mm long, 187 (max diameter 140 μm) in an individual 3.18 mm long while a still larger female (4.13 mm) had 318 eggs although these were at an earlier stage in development (max diameter 85 μm). This possibly suggests that the species breeds more than once in its life and that breeding is not synchronous.

In the course of growth, the rostrum becomes more pronounced and the posterior ventral sinuosity more concave (Fig. 20). As a result of the proportionate change in growth, the umbo becomes more central, lying immediately posterior to the mid point and the height/length ratio decreases from a mean value of 0.76 to a mean value of 0.69. The width-length ratio is maintained within the range 0.4–0.5.

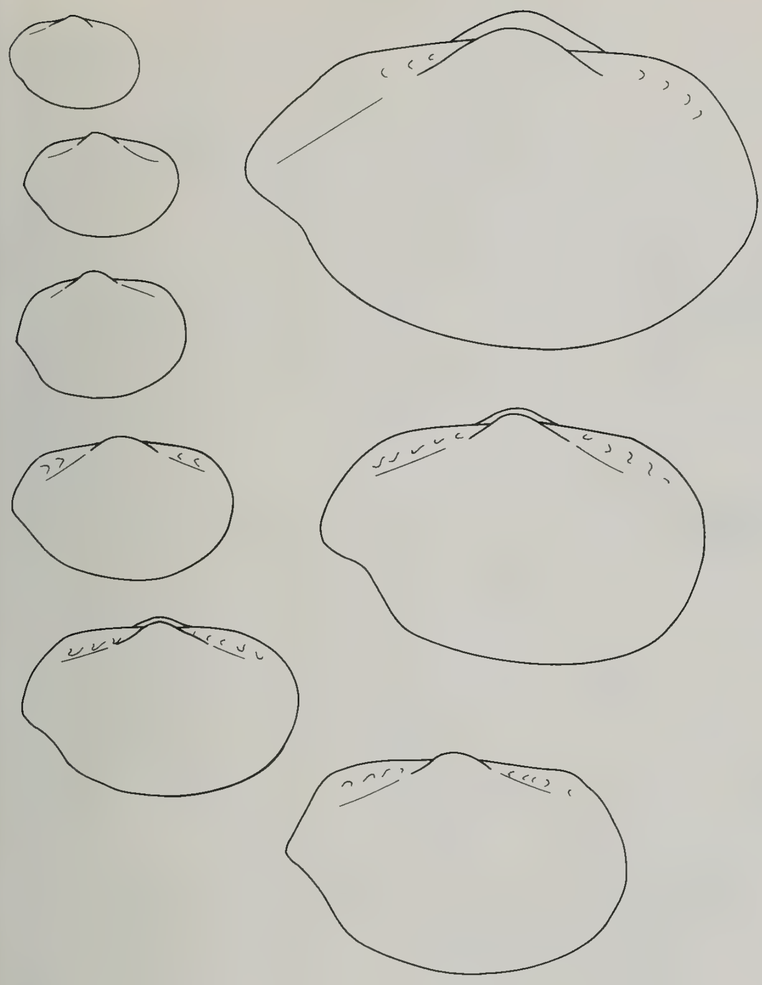

Fig. 20 *L. pustulosa marshalli*: Growth series of shells from Station 321 seen in outline from right side.

DISTRIBUTION. West European Basin—Rockall, Bay of Biscay, Southwest of Ireland. Abyssal rise to deepest abyssal depths.

DEPTH RANGE. 2466–4796 metres.

Ledella pustulosa argentinae new subspecies

HOLOTYPE. BM(NH) 1988084

TYPE LOCALITY. Station 247, Atlantis II, Cruise 60, 5208–5223 m, Argentine Basin.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			ARGENTINE BASIN				
Atlantis II	242	4382–4402	104	38°16.9′S	51°56.1′W	ES	13. 3.71
60	243	3820	41	37°36.8′S	52°23.6′W	ES	14. 3.71
	247	5208–5223	57	43°33.0′S	48°58.1′W	ES	17. 3.71
	256	3906–3917	97	37°40.9′S	52°19.3′W	ES	24. 3.71
	259	3305–3317	6	37°13.3′S	52°45.0′W	ES	26. 3.71

DESCRIPTION (Fig. 22). Shell, similar in shape to *L. p. marshalli*, surface more smooth with less conspicuous concentric ridges and radial striae, shell of valves slightly thicker, umbo more central, slightly more inflated; number of hinge teeth appear to intermediate between *L. p. pustulosa* and *L. p. marshalli*, however there was no significant difference between the teeth number/length measurements of the three subspecies.

Larval shell length 240 μm, maximum recorded length 4.74 mm.

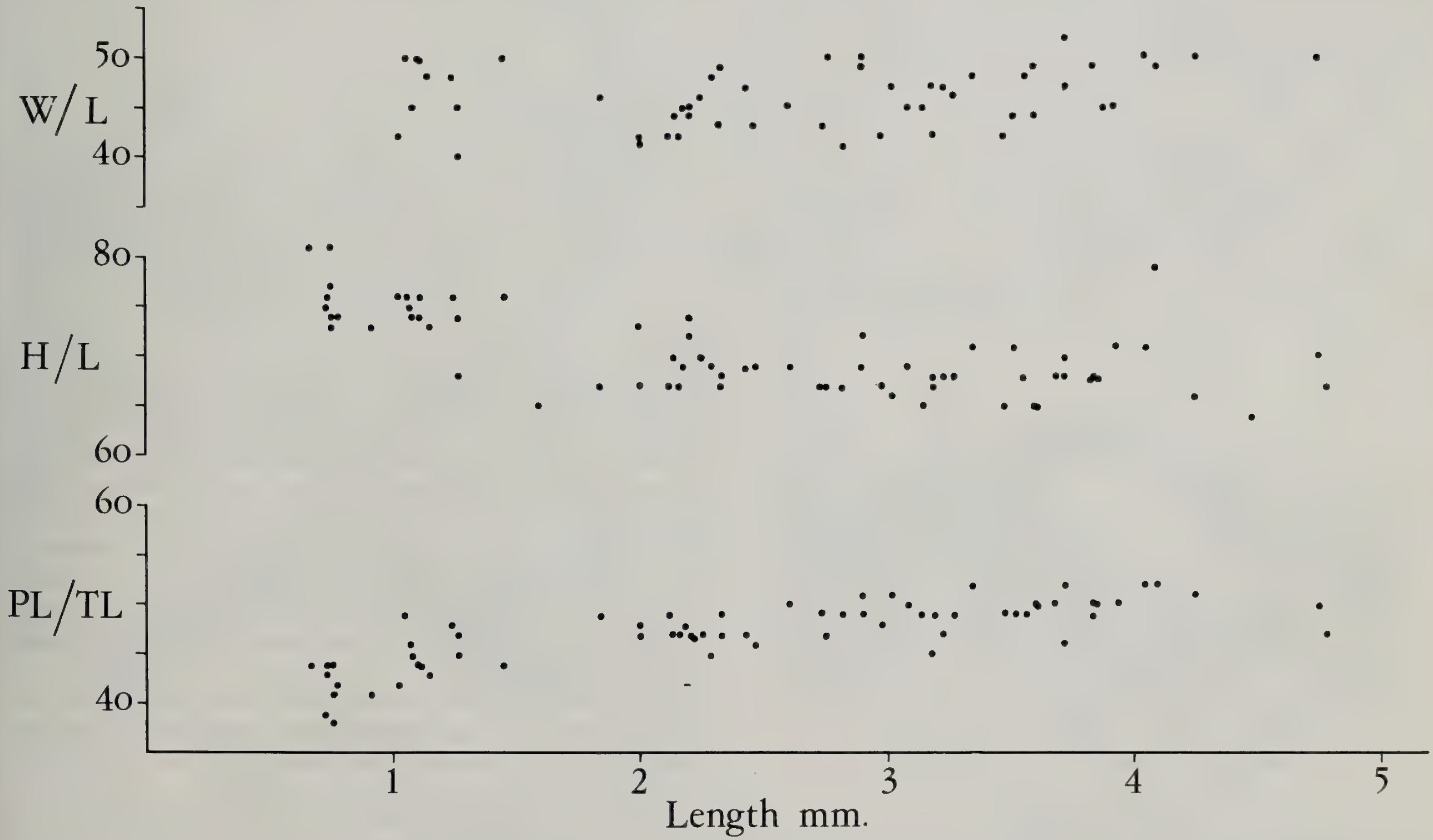

Fig. 21 *L. pustulosa marshalli*: An analysis of change in shape with growth as shown by the plots of the ratios, post-umbo length/length (PL/TL); height/length (H/L) and width/length (W/L) against length for specimens from Sta. 321.

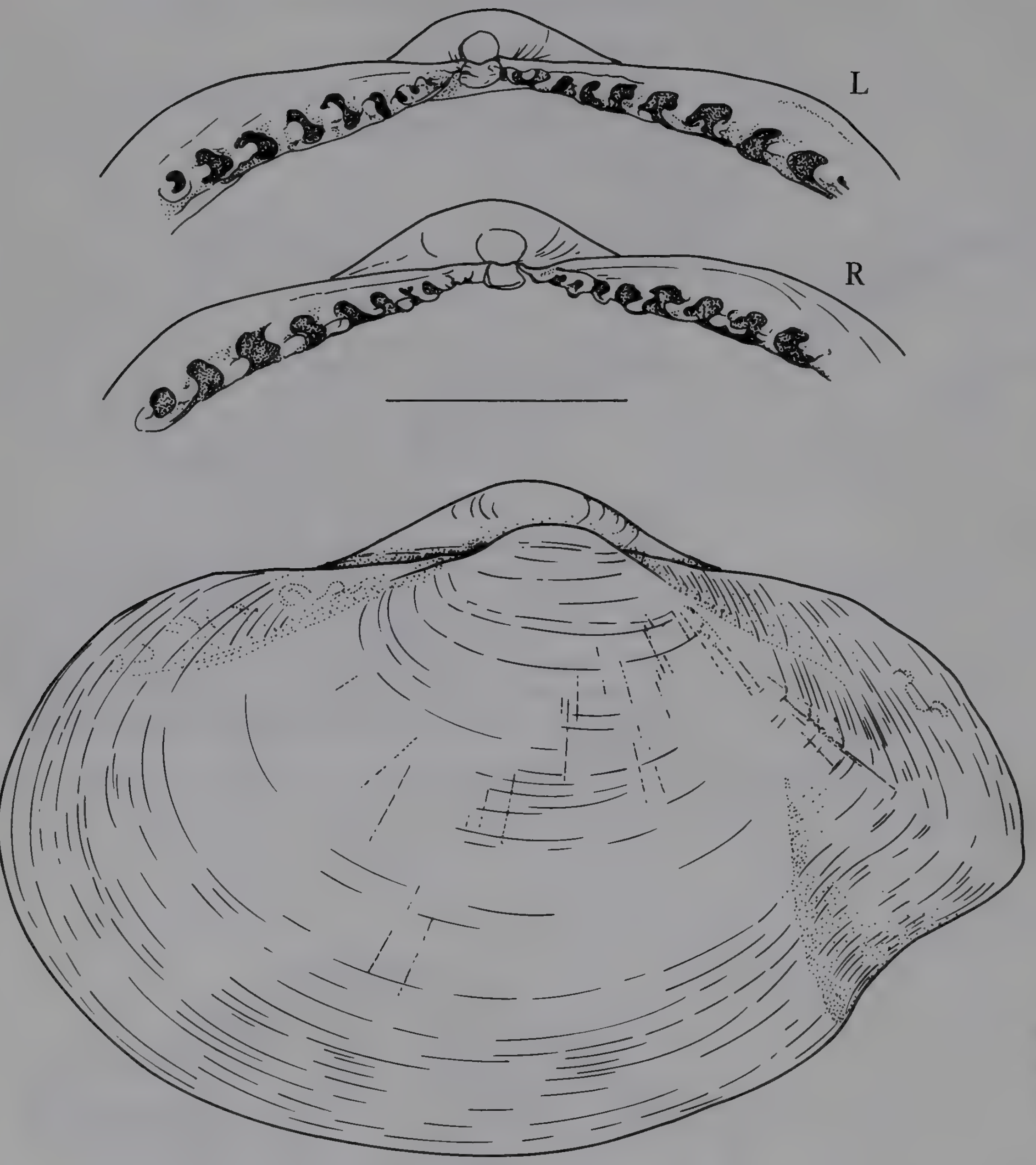

Fig. 22 *L. pustulosa argentinae*: Left lateral view of shell from Atlantis II, Sta. 247, and detail of hinge plates of right and left valves of the holotype. (Scale = 1 mm).

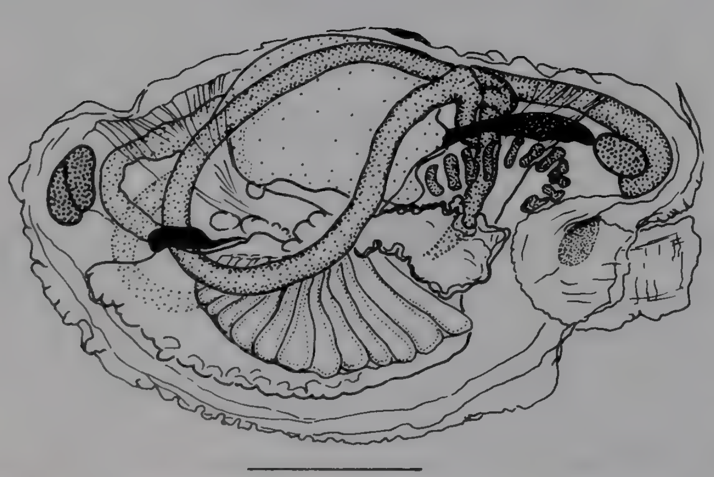

Fig. 23 *L. pustulosa argentinae*: Lateral view of specimen from left side with shell removed to show arrangement of body organs. (Scale = 1 mm). For identification of parts see Fig. 5.

The basic body form while similar to that of *L. p. pustulosa* has several slight differences (Fig. 23). The adductor muscles are larger and the posterior, in particular, is more rounded in outline than in the previously two subspecies. The labial palps have fewer (7–12) but broader ridges and the number of gill filaments (8–13) is also less. Posterior to the foot, the inner demibranchs appear to interlock and provide a channel for the faeces between the anus and siphon. There is a large byssal gland. The nervous system is well developed with large visceral and cerebral ganglia. The pedal ganglia are also large and lie high in the foot.

The smallest specimen seen with developing gonads was 1.9 mm long. The ova number varies from 55 (2.1 mm total length) to 169 (4.4 mm total length) and the egg lengths within the individual containing the largest ova varied from 150–180 µm. In this individual (3.00 mm total length), some eggs had been released and were lying cradled in the gill filaments close to the siphon.

In the course of growth, the anterior margin becomes more

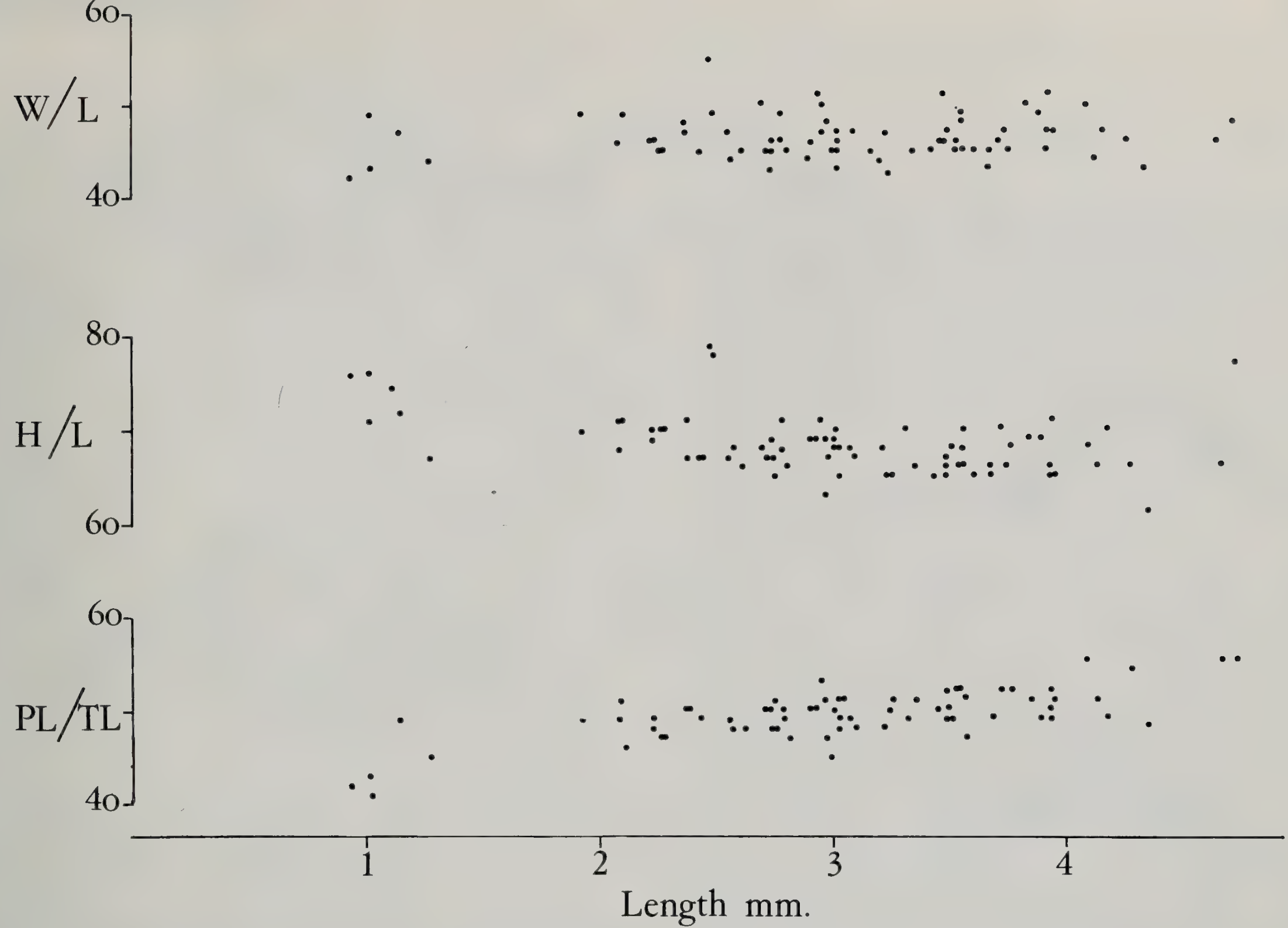

Fig. 24 *L. pustulosa argentinae*: An analysis of change in shape with growth as shown by the ratios, post-umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 242.

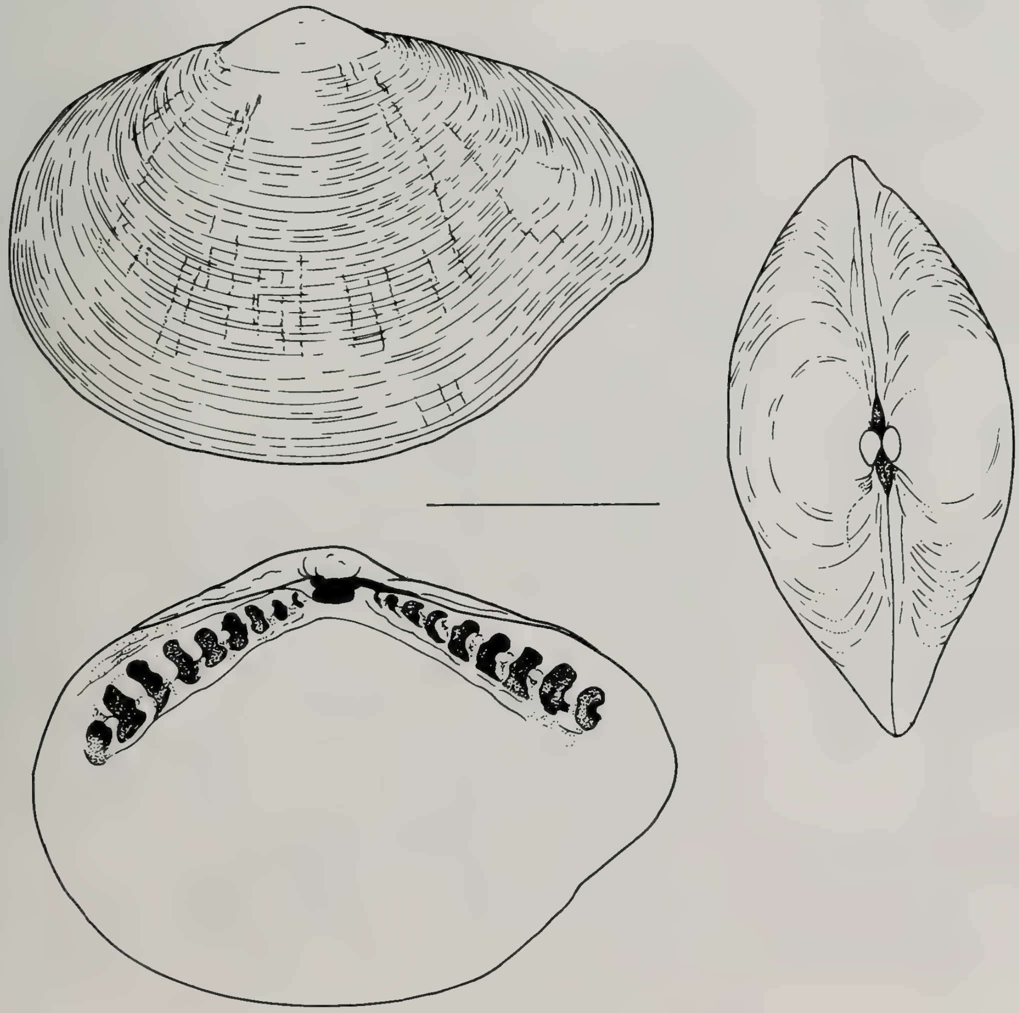

Fig. 25 *L. pustulosa hamsoni*: Left lateral external view of shell from Atlantis II, Station 144, lateral view of right valve of same shell and dorsal view of shell from Atlantis II, Station 141. (Scale = 1 mm).

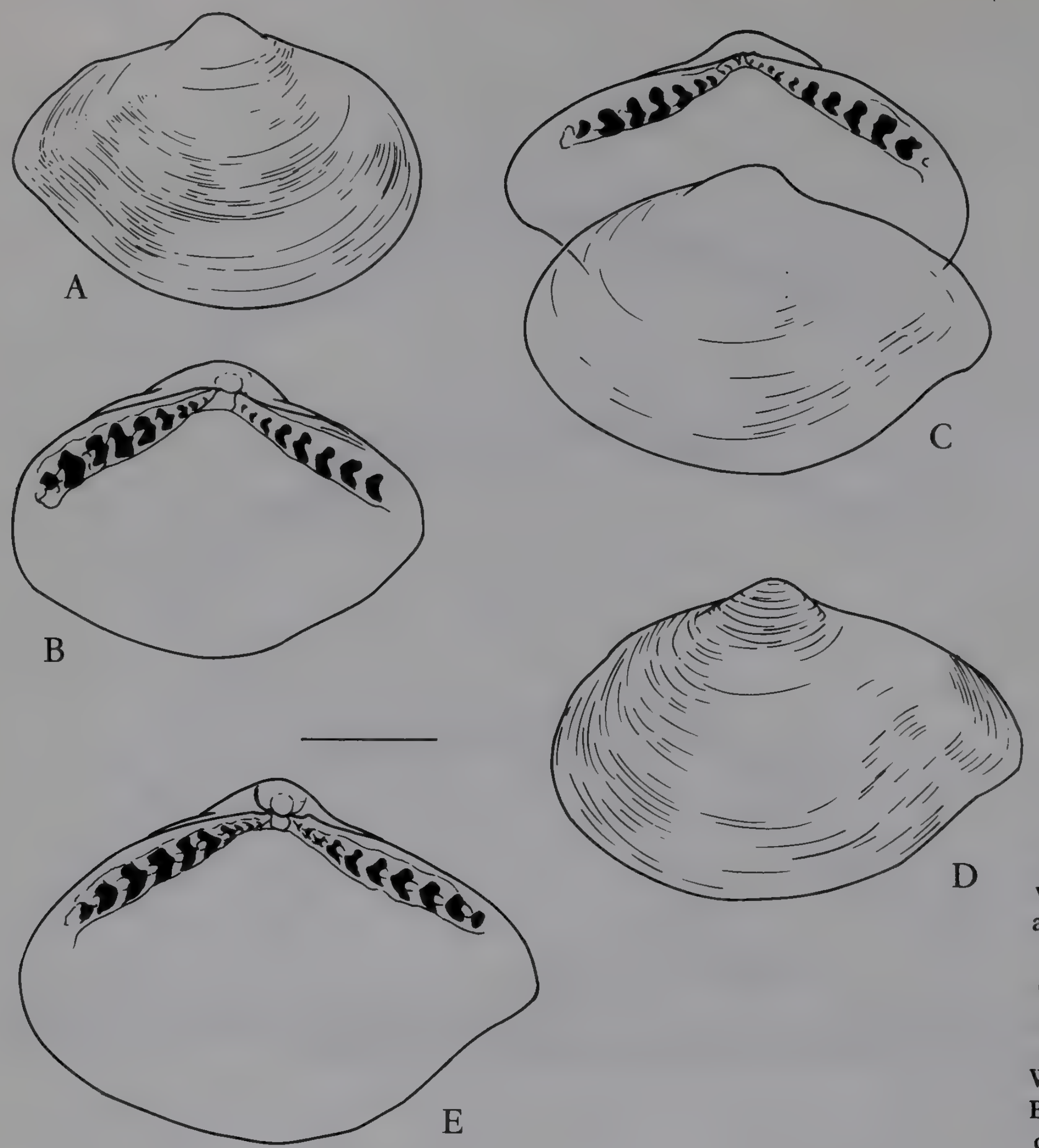

Fig. 26 *Ledella sublevis*: a) Lateral external view of holotype specimen (USNM No. 35212) as seen from right side; b) Lateral internal view of right valve of same specimen; c) Lateral external view and internal view of left valve of specimen (USNM No. 199689) labelled *Leda acuminata* but relabelled *Ledella sublevis* by Warén; d) Left lateral view of shell from Station Biogas III DS41, and e) Internal view of left valve of specimen from Station 262. (Scale = 1 mm).

smoothly curved and the ventral sinuosity more pronounced. The ratios of height/length, width/length and posterior umbonal distance/total length against length of this subspecies are similar to those of *L. p. pustulosa* and *L. p. marshalli* (Fig. 24).

DISTRIBUTION. Argentine Basin. Abyssal depths.

DEPTH RANGE. 3305–5223 metres.

Ledella pustulosa hampsoni new subspecies

HOLOTYPE. BM(NH) 1988085

TYPE LOCALITY. Station 144, Atlantis II, cruise 31, 2052–2357 m, 10°36.0′N 17°49.0′W, off West Africa.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			CAPE VERDE BASIN				
Atlantis II	141	2131	2	10°30.0′N	17°51.5′W	ES	5.2.67
31	144	2051–2357	3	10°36.0′N	17°40.0′W	ES	5.2.67
	145	2105–2192	1	10°36.0′N	17°49.0′W	ES	6.2.67

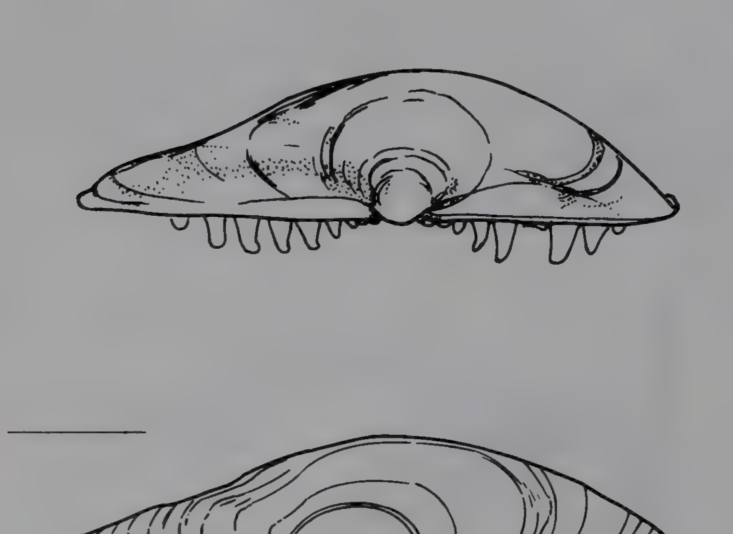

Fig. 27 *Ledella sublevis*: Dorsal view of an intact shell and a left valve from Station Biogas III DS41. (Scale = 1 mm).

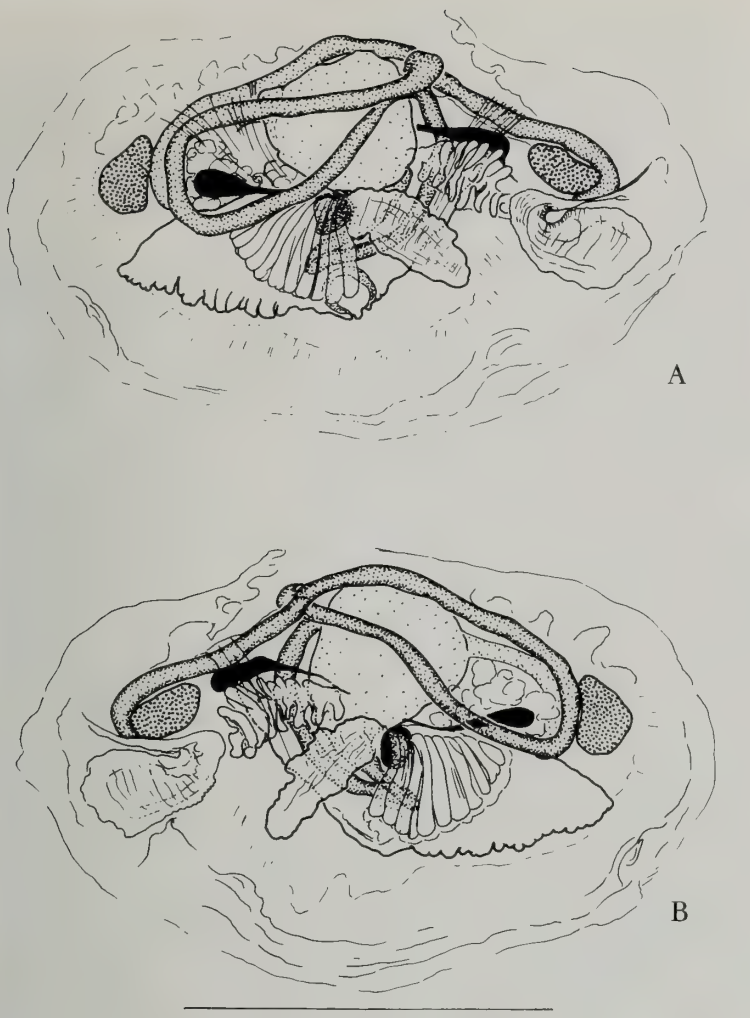

Fig. 28 *Ledella sublevis*: Lateral views of specimen from (a) left and (b) right sides with shell removed to show arrangement of the body organs. (Scale = 1 mm). For identification of parts see Fig. 5.

DESCRIPTION (Fig. 25). Shell shape while variable most closely resembles *L. p. pustulosa*, radial striae present, more conspicuous and irregular concentric ridges than other subspecies, also shell of valves much thicker, stronger; broader hinge plate; unlike other subspecies internal ligament approximately rectangular in shape, restricted to upper half of hinge plate with small external part on either side of the beaks.

Larval shell length 150 μm, maximum recorded length 2.67 mm.

The shape of the hinge of this subspecies resembles that of the fossil described by Seguenza (1877) (Fig. 17). Because of the small number of specimens available only a limited comparison of the internal morphology with *L. p. pustulosa* was possible. The byssal gland is relatively small; there are 10–12 gill filaments and 10–14 palp ridges. The hind gut configuration is similar with loop on either side of the body. The visceral and cerebral ganglia are moderately small and club-shaped.

Gonads were not seen in an individual 1.7 mm in length but could be seen in an individual 2.2 mm in length. In the latter specimen the testis partially surrounds the hind gut loops and the digestive diverticula and lies dorsal to the viscera between the anterior adductor muscle and the resilium.

DISTRIBUTION. Off the West coast of Africa. Abyssal rise.

DEPTH RANGE. 2051–2357 metres.

Ledella sublevis Verrill & Bush, 1898

HOLOTYPE. USNM No. 35212.

TYPE LOCALITY. U.S. Fish Comm. Sta. 2689, off Martha's Vineyard, 960 m.

SYNONYMY. *Leda acuminata* Jeffreys, 1870 (in part) *Ann. Mag. nat. Hist.* Ser. 4, *6*, p. 69.
Leda messanensis Jeffreys, 1879 (in part). *Proc. zool. Soc. Lond.* p. 576.
Ledella messanensis var *sublevis* Verrill & Bush, 1898. *Proc. U.S. natl., Mus.*, *20*, p. 856, pl. 81, Fig. 7.
Leda (Ledella) modesta Thiele & Jaeckel, 1931. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'*, 21, p. 44, pl. 2. Fig. 50.
Ledella ultima (Smith): Knudsen, 1970. *Galathea Rept.*, *11*, p. 34, Figs. 17 & 18, pl. 2, Fig. 15, pl. 3. Fig. 4.
Ledella sublaevis (Verrill & Bush): Warén, 1978. *Sarsia*, *63*, p. 214, Figs. 14 & 15.

This species has been much confused with *L. ultima* (p. 155) and *L. acuminata* (p. 153). Indeed, Verrill (1884) and Verrill & Bush (1887, 1898) who recognized differences from *L. ultima* (*L. messanensis* as they thought) were not entirely sure and persisted in referring to the species as a variety. This was largely because there were very few specimens of *L. sublevis* present among many of *L. ultima* in mixed samples. Unfortunately they did not examine the morphology of the body organs. Curiously, even Knudsen (1970) who did examine the body considered that *L. modesta, L. ultima* and his specimen of *L. sublaevis* from the 'Galathea' Expedition to be conspecific. Having examined the types of *L. ultima* and *L. modesta* we disagree. The latter is without doubt distinct species however, *L. modesta* is conspecific with *L. sublevis*. The identification of the 'Galathea' specimen is somewhat unclear, but from Knudsen's description it would appear to us to be *L. sublevis*. Clarke (1961b) who also combined *L. modesta* with *L. ultima* additionally included *L. spreta* (Thiele & Jaeckel 1931) in his synonomy. His description agrees closely with that of *L. ultima* (Smith) and with our extensive collections of *L. ultima*. Having examined specimens of *L. spreta*, like Knudsen (1970) and Barnard (1964) before him, we consider it to be a separate species. We confirm the description by Warén (1978) and agree with him in raising the Verrill & Bush variety to species status but, correct his spelling to that of the original. The drawings by Warén (1978) are excellent in their accuracy.

MATERIAL. USNM No. 199689 labelled *Leda acuminata* (figured by Warén, 1978).

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
				WEST EUROPEAN BASIN			
Sarsia	S50	2379	6	43°46.7′N	3°38.0′W	ED	18. 7.67
Chain 106	321	2868–2890	3	50°12.3′N –50°08.3′N	13°35.8′W –13°53.7′W	ES	20. 8.72
	323	3356–3338	4	50°08.3′N –50°04.9′N	13°50.9′W –14°23.8′W	ES	21. 8.72
	326	3859	12	50°05.3′N	14°24.8′W	ES	22. 8.72
	330	4632	1	50°43.5′N –50°43.4′N	17°51.7′W –17°52.9′W	ES	24. 8.72
Jean Charcot (Biogas III)	DS38	2138	2	47°32.5′N	8°35.8′W	DS	25. 8.73
	DS41	3548	22	47°28.3′N	9°07.2′W	DS	26. 8.73
(Biogas IV)	DS57	2906	2	47°30.8′N	9°07.6′W	DS	23. 2.74

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
	DS60	3742	6	47°26.8′N	9°07.2′W	DS	24. 2.74
	DS63	2126	1	47°32.8′N	8°35.0′W	DS	26. 2.74
	CP01	2245	1	47°34.6′N	8°38.8′W	CP	25. 2.74
(Biogas V)	DS66	3480	1	47°28.2′N	9°00.0′W	DS	16. 6.74
(Biogas VI)	DS73	2805	1	47°32.1′N	9°06.0′W	DS	21.10.74
GUINEA BASIN/SIERRA LEONE BASIN							
(Walda)	DS20	2514	1	2°32.0′S	8°18.1′E	DS	
	DS25	2470	34	2°19.8′S	7°49.2′E	DS	
NORTH AMERICA BASIN							
Atlantis 273	GH*2	2488	1	39°26.0′N	70°34.0′W	AD	3.10.61
Atlantis II 12	62	2496	3	39°26.0′N	70°33.0′W	ES	21. 8.64
	64	2886	7	38°46.0′N	70°06.0′W	ES	21. 8.64
	70	4680	1	36°23.0′N	67°58.0′W	ES	23. 8.64
	72	2864	6	38°16.0′N	71°47.0′W	ES	24. 8.64
Chain-50	76	2862	10	39°38.3′N	67°57.8′W	ES	29. 6.65
	85	3834	3	37°59.2′N –39°37.0′N	69°26.2′W –66°47.0′W	ES	5. 7.65
Chain-58	103	2022	4	39°43.6′N	70°37.4′W	ET	4. 5.66
	115	2031–2051	1	39°39.2′N	70°24.5′W	ET	16. 8.66
Atlantis II 24	126	3806	8	39°37.0′N –39°37.5′N	66°47.0′W –66°44.0′W	ES	24. 8.66
Atlantis II 30	131	2178	22	39°38.5′N –39°39.0′N	70°36.5′W –70°37.1′W	ES	18.12.66
	340	3264–3356	15	38°14.4′N –38°17.6′N	70°20.3′W –70°22.8′W	ES	24.11.73
CAPE VERDE BASIN							
Atlantis II 31	147	293	27	10°38.0′N	17°52.0′W	ES	6. 2.67
ARGENTINE BASIN							
Atlantis II 60	239	1661–1679	142	36°49.0′S	53°15.4′W	ES	11. 3.71
	140	2195–2323	18	36°53.4′S	53°10.2′W	ES	12. 3.71
	245	2707	8	36°55.7′S	53°01.4′W	ES	14. 3.71
	259	3305–3317	24	37°13.3′S	52°45.0′W	ES	26. 3.71
	262	2440–2480	220	36°05.2′S	52°17.9′W	ES	27. 3.71
	264	2041–2048	2	36°12.7′S	52°42.7′W	ES	28. 3.71
ANGOLA BASIN							
Atlantis II 42	200	2644–2754	7	9°43.5′S – 9°29.0′S	10°57.0′E –11°34.0′E	ES	22. 7.68

DESCRIPTION (Figs. 26a-e, 27). Shell moderately thick, elongate, oval with pointed rostrum, sculpture fine regular concentric ridges more prominent ventrally, several radial striae or wrinkles usually visible in oblique rostral depression; dorsal margin moderately convex, antero-dorsal margin slopes gradually from umbo to form smooth curve with anterior margin proximal, postero-dorsal margin gradually slopes from umbo to posterior limit of hinge plate distally then more sharply to form rostrum, posterior ventral margin sinuous, ventral margin smooth, moderately convex curve; umbo inflated, slightly inclined posteriorly, relatively more anterior in position in large specimens; keel extends from umbo to rostral tip, concentric ridges curve acutely at this point; hinge plate long, broad, anterior and posterior series of 6–12 strong, upright chevron-shaped teeth, the number vary with size; ligament amphidetic, internal part moderately large, approximately as long as wide, trapezoidal with truncated apex, extending externally for short distance on either side of umbo; pallial and sinus scar conspicuous in large specimens.

MORPHOLOGY. *Ledella sublevis* has a similar morphology to *L. pustulosa* (Figs. 19 & 28a & b). Of the mantle structures, the wall of the combined siphon is thick and muscular with a well developed feeding aperture ventral to it. The siphonal tentacle originates on the left side of the siphonal embayment. The adductor muscles are almost equal in size, the anterior being the slightly larger.

The gills have approximately 14 plates to each demibranch. In this species they do not appear to interlock posterior to the foot but this may be a matter of change following fixation. The palps are small, with 12 ridges in the largest specimens.

There is a large 'byssal' gland in the heel of the foot. The large stomach has six sorting ridges, and together with the style sac, is similar to that described for *L. pustulosa*. The style sac penetrates the ventral half of the foot (Figs. 28a & b) and there are single loops of hind gut on each side of the body. The course of the hind gut differs somewhat from that of *L. pustulosa* in that having passed from the left side of the body to the right the gut takes an anterior and horizontal course for a short distance before forming the right loop.

The ganglia are well developed. The kidney is large with a ventral lobe penetrating the foot posterior to the style sac.

During growth the rostrum becomes more pronounced with a gradual increase in the umbo-rostral length/total length ratio with increasing length (Fig. 29). At the same time there is also a decrease in the height to length ratio with increasing length. There is little change in the width to length ratio.

The smallest specimen with developing gonads was 2.5 mm total length (Station 262, Argentine Basin). The sexes are separate, with males and females in approximately equal number. The number of ova increases from 102 (2.5 mm length) to 265 (4.2 mm length), but the maximum size of the ova varied little between individuals of different sizes (140–160 μm).

DISTRIBUTION. North East and West Atlantic and Argentine Basin.

DEPTH RANGE. 2022–4680 m.

This species differs from other species of *Ledella* in having a smoother, thicker, more inflated shell, in which the concentric ridging is much less pronounced. It is more elongate than *L. ultima* with a more pointed rostrum. Other characteristic features are the broad hinge plate and the small but clearly visible external part of the ligament. The type of gut configuration is similar to that of the *L. pustulosa* complex.

There are some population differences in the specimens from the Argentine basin as compared with elsewhere. While the internal morphology is identical externally the Argentine shells are slightly thinner and differ slightly in their shape, being somewhat more elongate, and in the thickness of the hinge plate and the form of the ligament, and but for the differences in internal morphology might be confused with *L. acuminata*.

Ledella jamesi new species

HOLOTYPE. BM(NH) 1988087

TYPE LOCALITY. Knorr 25, Station 299, 7°55.1′N, 55°43.0′W, 1942–2076 m, Guiana Basin.

SYNONYMY. *Nuculana A.* James 1972 Thesis, Texas A & M. Univ. p. 126. Figs. 79–81.

MATERIAL.

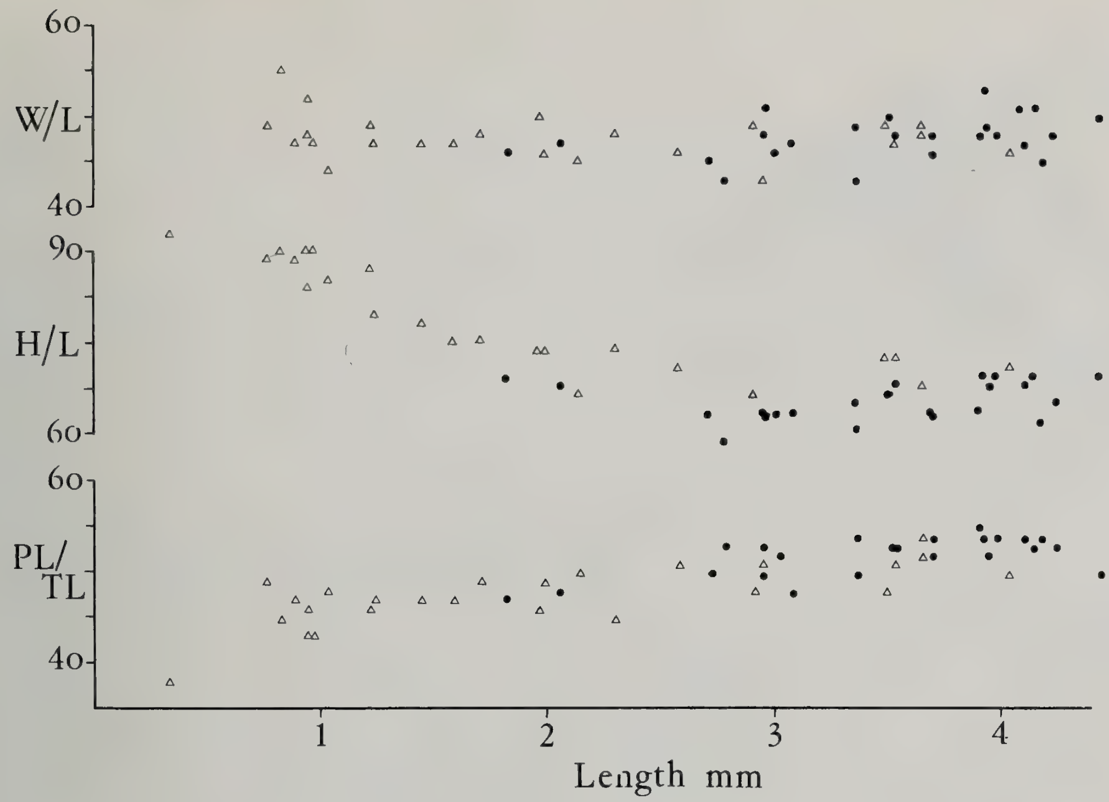

Fig. 29 *Ledella sublevis*: An analysis of change in shape with growth as shown by the ratios, posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Stations Walda DS25 (closed circles) and 259 (open triangles).

Cruise	Sta	Depth(m)	No	Lat.	Long.	Gear	Date
		ARGENTINE BASIN					
Atlantis II	239	1661–1679	889	36°49.0′S	53°15.4′W	ES	11. 3.71
60	240	2195–2323	61	36°53.4′S	53°10.2′W	ES	12. 3.71
	262	2440–2480	3	36°05.2′S	52°17.9′W	ES	27. 3.71
	264	2041–2048	8	36°12.7′S	52°42.7′W	ES	28. 3.71
		GUIANA BASIN					
Knorr 25	293	1456–1518	2	8°58.0′N	54°04.3′W	ES	27. 2.72
	299	1941–2076	566	7°55.1′N	55°42.0′W	ES	29. 2.72
	301	2487–2500	51	8°12.4′N	55°50.2′W	ES	29. 2.72
	303	2842–2853	268	8°28.8′N	56°04.5′W	ES	1. 3.72

James (1972) gives a description of valves of this species taken from depths of 752–527 m in the Gulf of Mexico, in her thesis on the protobranch molluscs from the deep waters of the Gulf.

Description (Figs. 30a & b). Shell inequilateral, moderately inflated, approximately oblong, somewhat variable in outline with short pointed rostrum, sculpture prominent, slightly irregular concentric ridges with radial striations in posterior depression in front of keel; umbo slightly posterior to mid line in small specimens, anterior in larger ones (ratio posterior umbonal to total length 0.39 in specimen 0.66 mm and 0.56 in specimen 2.84 mm), low in profile, medially directed; dorsal shell margins slope gently from umbos, anterior dorsal margin short, proximally slopes gradually then somewhat angular to curve of anterior margin, thus the anterior margin does not form a smooth curve, but ventrally forms part of evenly curved ventral margin, posterior dorsal margin curves gradually to point approximately level with second distal tooth then angles and forms convex dorsal edge of rostrum, ventral margin sinuous marking ventral limit of rostrum; moderate keel from umbo to tip of rostrum, concentric ridges curve through 90° over keel; hinge plate moderately broad, anterior

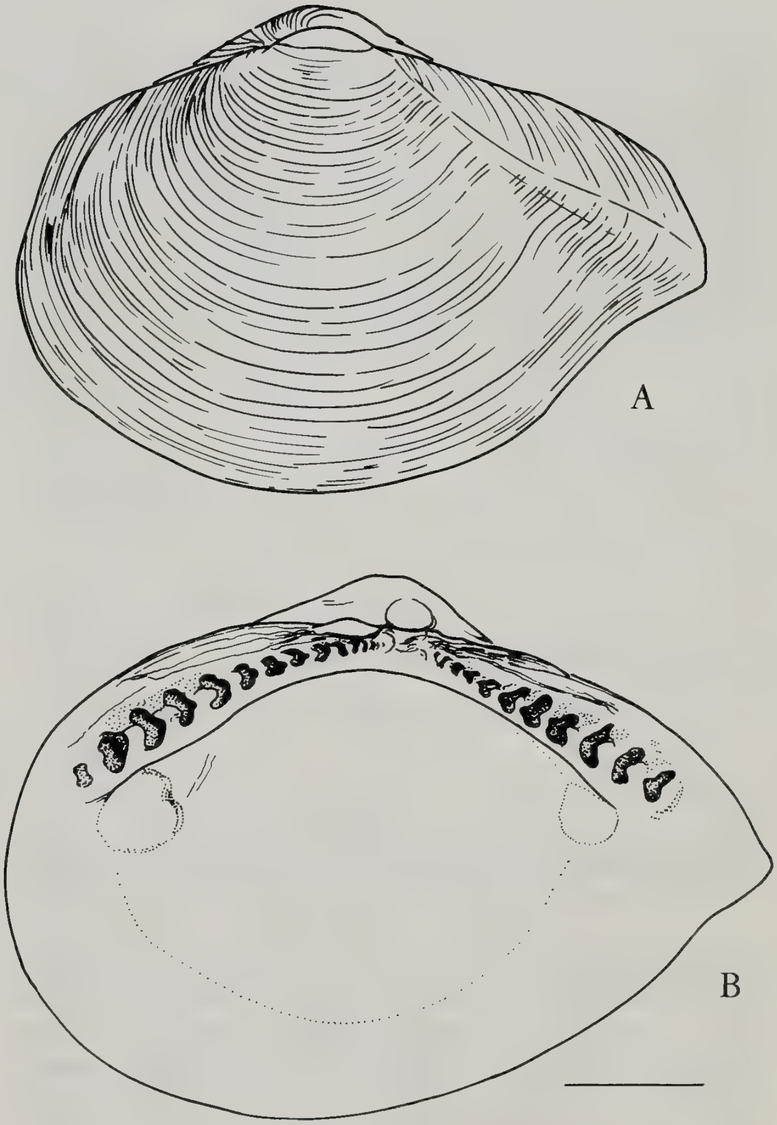

Fig. 30 *Ledella jamesi*: (a) Left lateral external view of the shell from Station 301; (b) Internal lateral view of right valve from Station 301. (Scale = 1 mm).

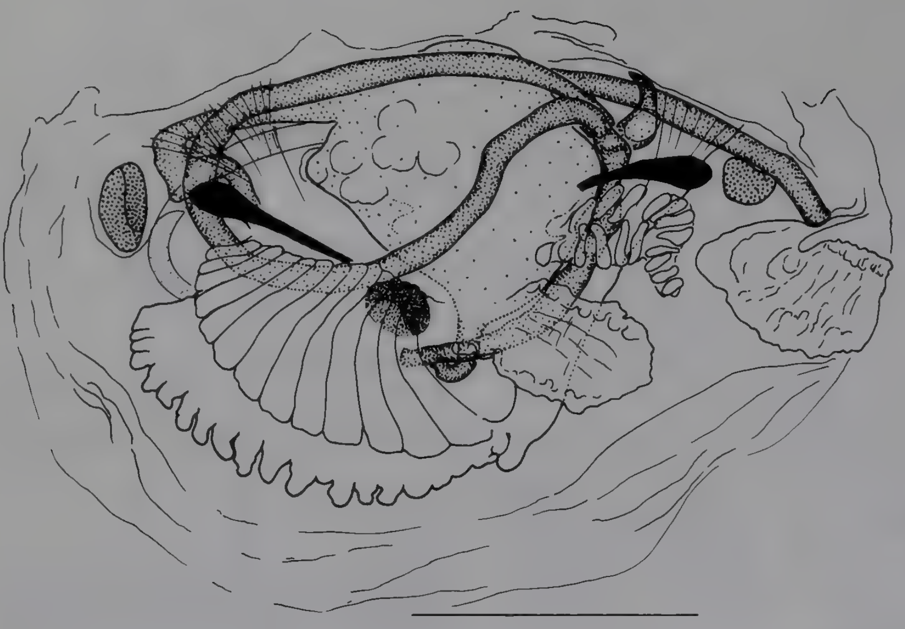

Fig. 31 *Ledella jamesi*: Lateral view of specimen from the left side with shell removed to show arrangement of the body organs. (Scale = 1 mm). For identification of parts see Fig. 5.

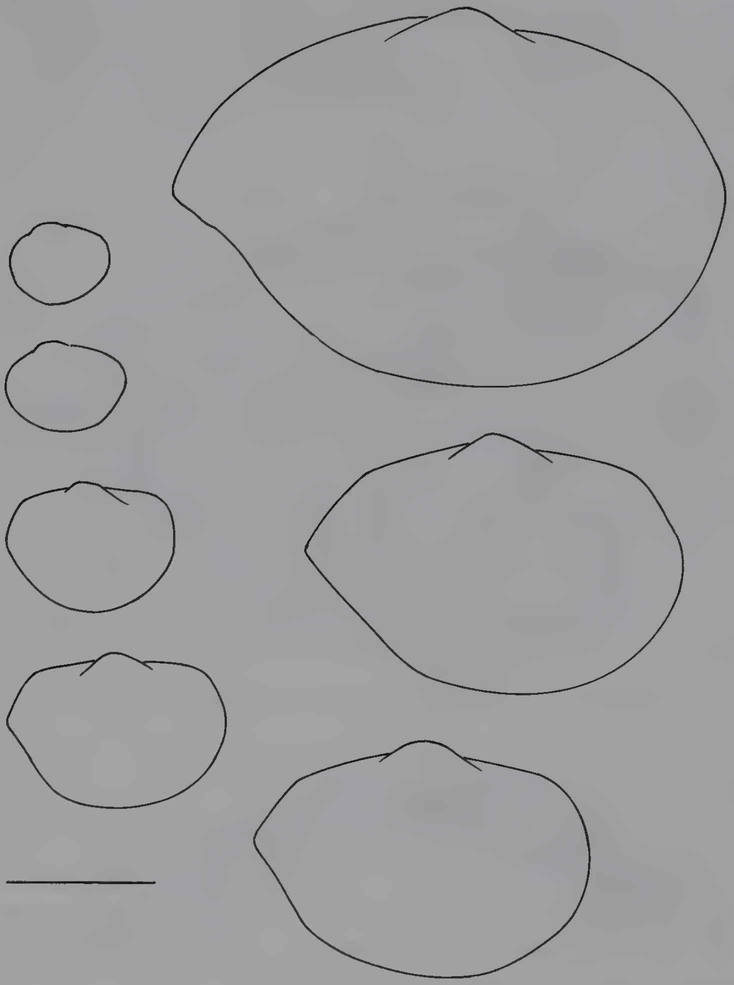

Fig. 32 *Ledella jamesi*: Growth series of shells from Station 239 in lateral outline to show change with increasing size. (Scale = 1 mm).

and posterior parts with 7–11 strong chevron teeth, the number varying with size of shell; ligament amphidetic, inner part approximately rectangular in shape, external part extending very short distance on either side of umbos; internally shell white and glossy, adductor scars and pallial line visible externally; periostracum cream with 'tortoise shell' pattern effect in some specimens.

Larval shell length 150 μm, maximum shell length 5.48 mm.

INTERNAL MORPHOLOGY. The basic form of the body is similar to *L. pustulosa* (Figs. 11 & 31). The middle and inner folds of the mantle are relatively well devloped. The anterior sense organ lies far forward, anterior to the anterior adductor muscle. The adductor muscles are relatively small, the anterior being larger than the posterior. The combined siphon is deep, but the musculature is less well developed than that in *L. pustulosa*. In most specimens the siphonal tentacle is on the right side.

The gills are moderate in size with approximately 14 plates to each demibranch. Posteriorly the inner demibranchs lie close together beside the internal edge of the siphon. In some sections the frontal cilia appear to interlock and possibly, in part, function to guide the faecal rods to the siphon. The palps are large with 14–20 ridges, the number varying with the size of the individual. The palp proboscides are also relatively large.

The foot is well developed and anteriorly directed. A small 'byssal' gland lies at the junction of the well developed heel region from the rest of the foot. The foot has many fringing papillae which are particularly long and conspicuous in this species. The form suggests a particularly active mode of life. Possibly correlated with this is a well developed nervous system. The cerebral, visceral, and pedal ganglia are particularly large, the cerebral and visceral being elongate and the joining commissures being particularly stout.

The digestive tract is similar to that in *L. pustulosa*. There is a large stomach with 6–7 sorting ridges externally visible. The style sac penetrates deep into the foot. The hind gut, which can be seen through the shell, forms two loops, one on each side of the body. As in *L. pustulosa* (Fig. 11) the course of the hind gut is somewhat variable with one or both loops either deformed or abnormally twisted.

Developing gonads were observed in animals greater than 2.0 mm in length. Approximately equal numbers of males and females were recorded. In sections the percentage of the body space filled by the testis increased from about 14.5% in a specimen 2.0 mm in length to 40% in a specimen 3.7 mm in length. In even larger animals this percentage decreased, for example approximately 26% of the body space was occupied by testis in an individual 4.3 mm in length. From sections, a female 2.3 mm in length, contained 28 ova with a maximum length of 85 μm, while another, 3.3 mm in length, contained

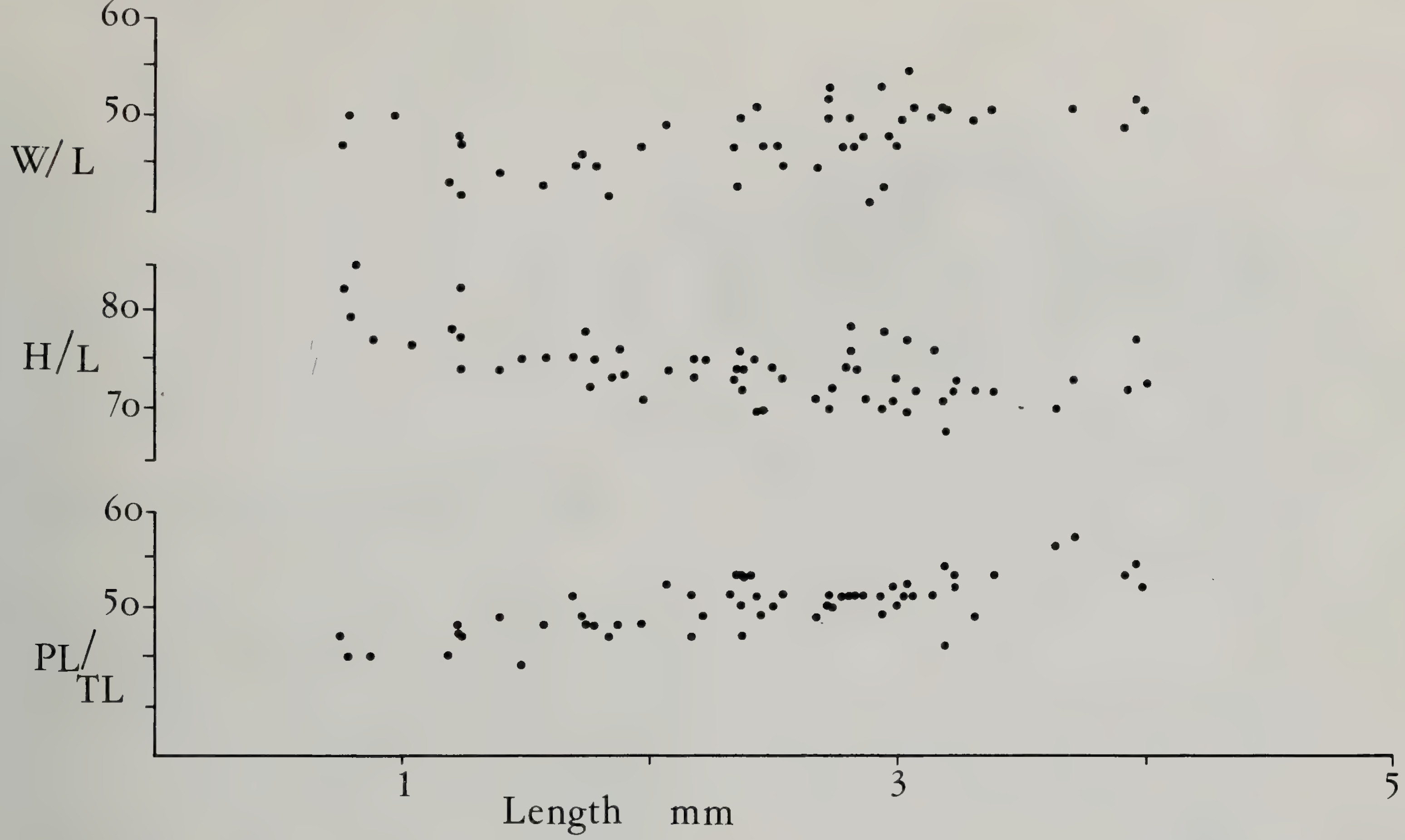

Fig. 33 *Ledella jamesi*: An analysis of change in shape with growth as shown by the ratios posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 239.

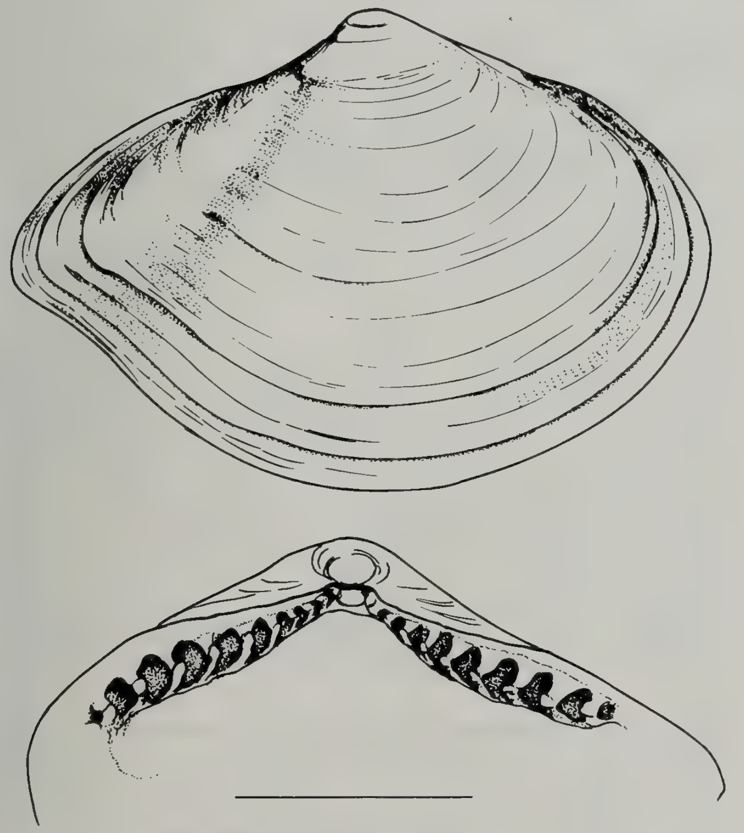

Fig. 34 *Ledella lusitanensis*: Right lateral external view of shell from Station 142 and internal view of hinge region of right valve from Station 142. (Scale = 1 mm).

219 ova with a maximum length 150 µm. Most ova were found posterior to the stomach.

In the course of growth, the rostrum becomes more pronounced with a gradual shift in the umbo-rostral length to total length ratio with increasing length. At the same time there is an overall decrease in the height/length ratio but in the width/length ratio changes little. The curvature of the dorsal margin also changes with age (Figs. 32 & 33). In young specimens it is distally straight and proximally angulate before curving to the anterior and posterior margins but with increasing age the dorsal margin becomes convex and with a more gradual curvature.

DISTRIBUTION. South and West Atlantic, Argentine and Surinam Basins and Gulf of Mexico.

DEPTH RANGE. 1456–2853 m.

Ledella lusitanensis new species

HOLOTYPE. BM(NH) 1988088; 2 Paratypes: BM(NH) 1988089

TYPE LOCALITY. Atlantis II Station 142, 10°30′N 17°51′W.

MATERIAL.

Cruise	Stn	Depth(m)	No	Lat	Long	Gear	Date
				WEST EUROPEAN BASIN			
Jean Charcot (Biogas VI)	CP24	1995	2	44°08.1′N	4°16.2′W	CP	31.10.74
				CAPE VERDE BASIN			
Atlantis II 31	142	1624–1796	28	10°30.0′N	17°51.5′W	ES	5. 2.67
	147	2934	18	10°38.0′N	17°52.0′W	ES	6. 2.67
				ANGOLA BASIN			
Atlantis II 42	194	2864	1	22°54.0′S	11°55.0′E	ES	17. 5.68

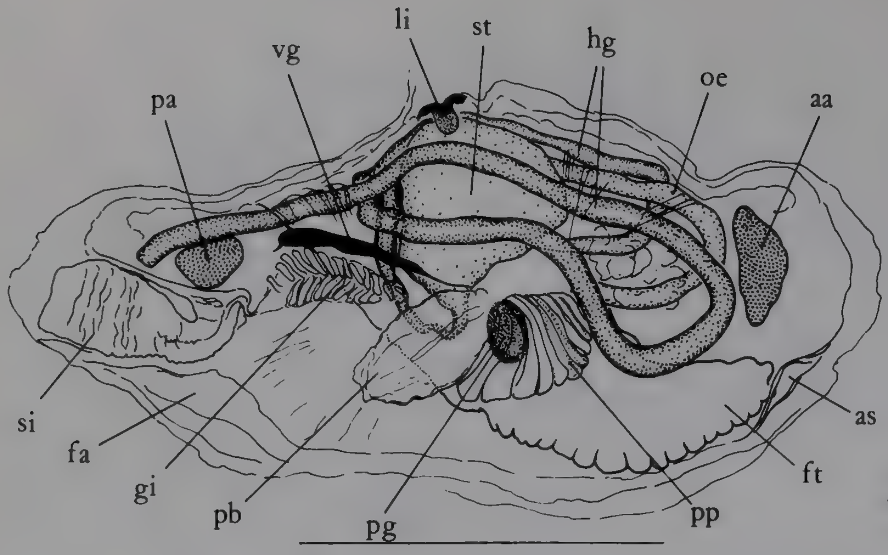

Fig. 35 *Ledella lusitanensis*: Lateral view of specimen from the right side with the shell removed to show the arrangement of the body organs. (Scale = 1 mm).

Description (Fig. 34). Shell moderately strong, inflated, almost equilateral, rostrum long, pointed; umbos slightly anterior in position, raised, posteriorly directed; shell ornamented with fine concentric ridges with superimposed pattern of light and darker bands of variable width; dorsal margin moderately convex, antero-dorsal margin slopes from umbo to anterior limit of hinge plate, then curves evenly to form rounded anterior margin, postero-dorsal margin proximally slopes gently, distally more acutely to form rostrum, posterior ventral margin not markedly sinuous, ventral margin long, smooth, moderately convex, moderate keel from umbo to point of rostrum; hinge plate very broad, strong, relatively long, anterior and posterior parts each with approximately 10 chevron teeth (number depending on size of animal), distal teeth extremely strong, well developed, proximal teeth progressively smaller, those bordering internal ligament small and rudimentary; ligament amphidetic, internal part rectangular, short external extensions, equal in length, on either side of umbos.

Larval shell length 190 µm; maximum recorded shell length 3.85 mm.

Morphology. Although the form of the body and mantle is similar to that of other species, the foot of *Ledella lusitanensis* is distinctive in being long, slender and having a more anteriorly directed attitude than that of other species described here (Fig. 35). The species is likely to have a very active mode of life. The foot itself is extremely muscular and the retractor muscles being particularly well developed. Correlated with this is a large oblong-shaped pedal ganglion, with other parts of the nervous system being generally well developed. A large byssal gland is present in the heel of the foot.

The siphon although poorly preserved in several preparations, is similar in structure to that described for *Ledella pustulosa* with large haemocoelic spaces between the muscle fibres. Considerable quantities of faecal material were found between the inner muscular lobes of the well developed feeding aperture but this is likely to have been an effect from the sample collection and processing. The siphonal tentacle is to the right side of the extreme inner limit of the siphonal embayment.

The gills are of moderate size with approximately 14 gill plates. The palps are similar to those of *Ledella sublevis* with 10–12 ridges. The stomach is large and well developed with

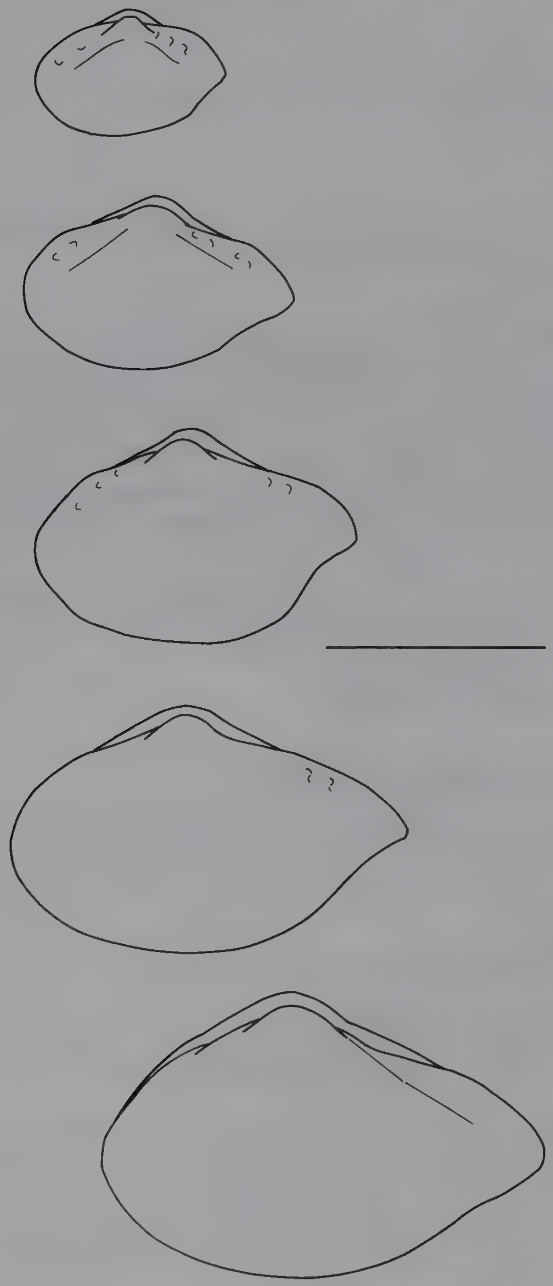

Fig. 36 *Ledella lusitanensis*: Growth series of shells from Station 142 in lateral outline to show change in shape with increasing size. (Scale = 1 mm).

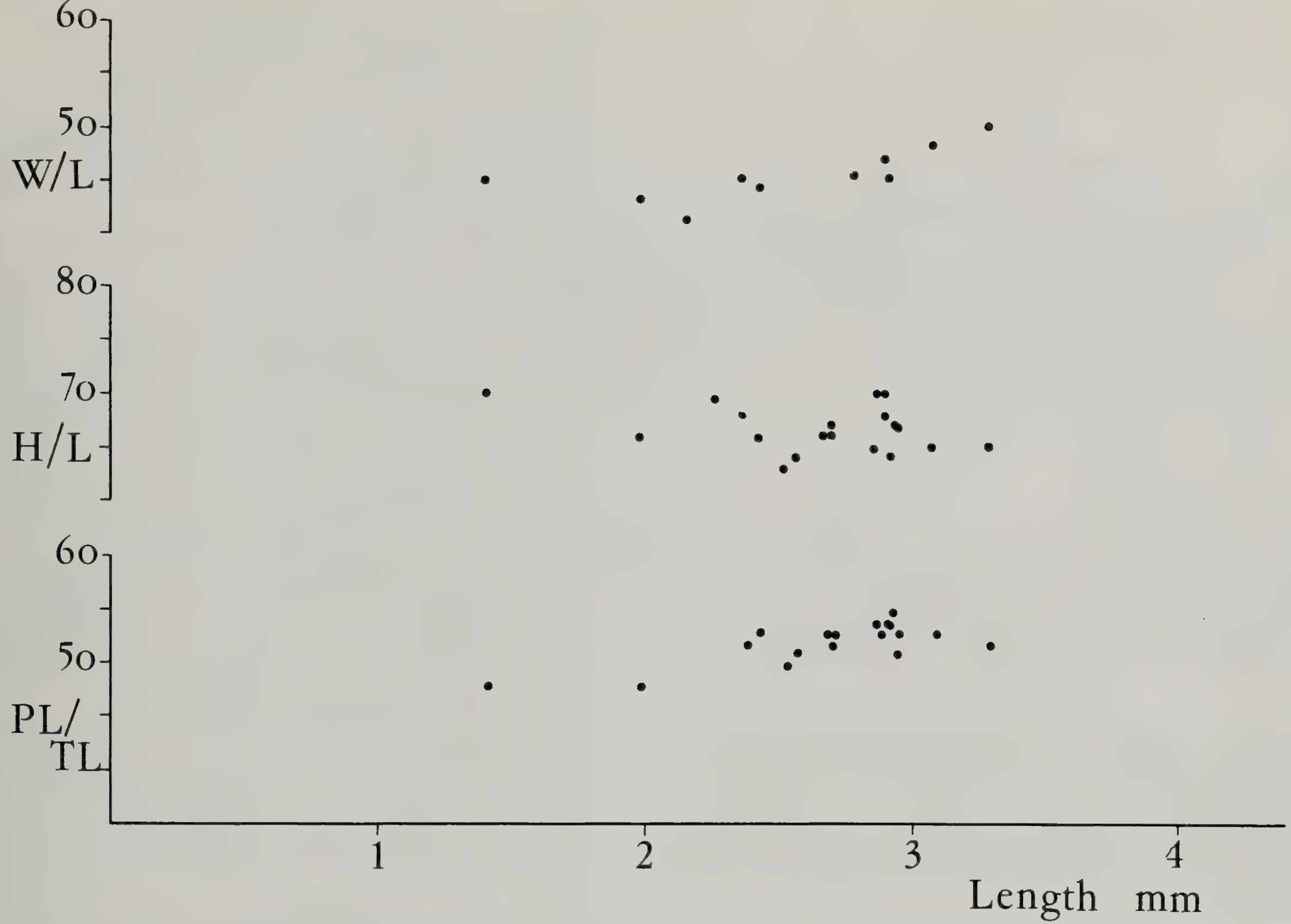

Fig. 37 *Ledella lusitanensis*: An analysis of change in shape with growth as shown by the ratios posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 142.

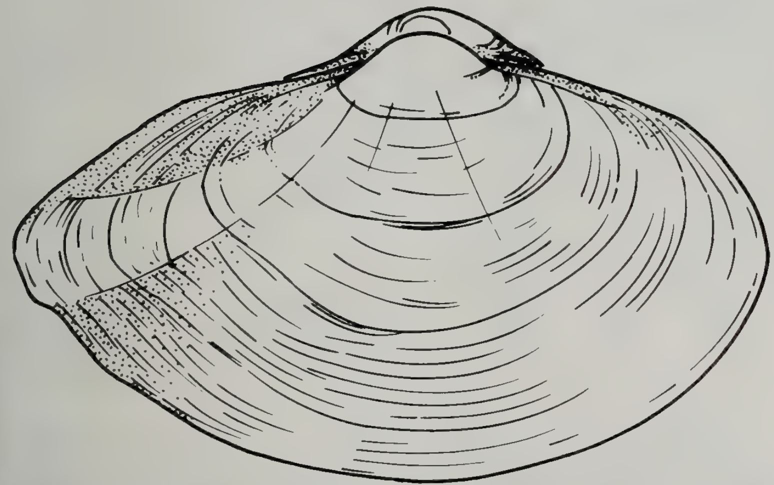

Fig. 38 *Ledella sandersi*: Right lateral external view of the shell from Station 191. (Scale = 1 mm).

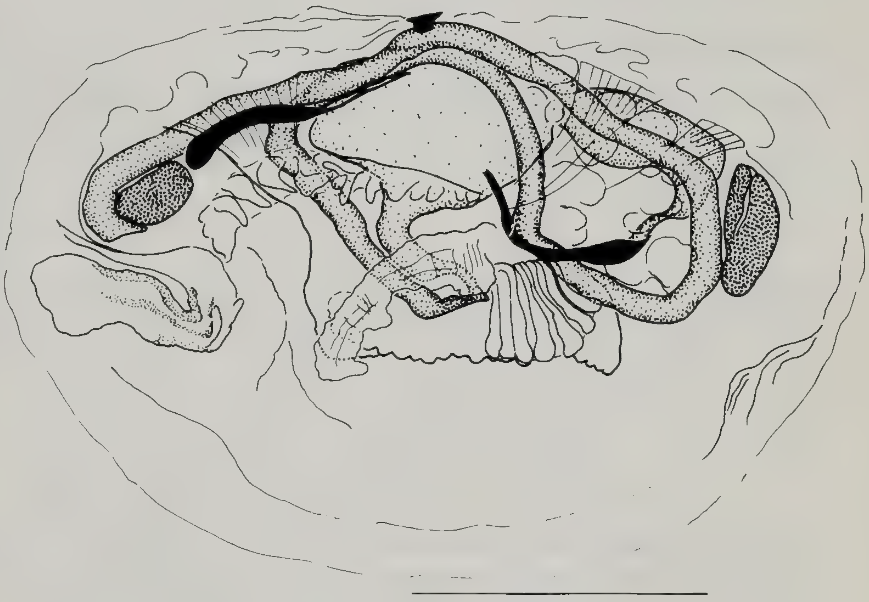

Fig. 39 *Ledella sandersi*: Lateral view of specimen from the right side with the shell removed to show the arrangement of the body organs. (Scale = 0.5 mm). For identification of parts see Fig. 35.

the openings to the left digestive diverticula dorsally on the left wall. One is immediately posterior and ventral to the oesophagus, the second is at approximately the same level and ventral to the tooth of the gastric shield. The shield is well developed. The style sac penetrates the upper half of between 1/3 – 1/2 of the ventral distance of the foot. The hind gut forms a single loop to each side of the body, the shape of the loops being similar to that of the right loop of *Ledella modesta*. The cross over point lies a short distance posterior to the ligament rather than immediately so as in *L. pustulosa*.

Few specimens of this species were intact and only two could be sectioned. Both were male, in the smallest (2.4 mm) the testis was slightly developed (2% of body area) while in the larger (3.1 mm) 16% of body area was covered by testis.

In the course of growth, the rostrum becomes more elongate with a slight shift in the total length/umbo-rostral length ratio (Figs. 36 & 37) and the dorsal margin becomes less convex. There is little change in the height/length and the width/length ratios.

This species is somewhat similar in appearance to *L. sublevis* but the shell is slightly smoother, more elongate and

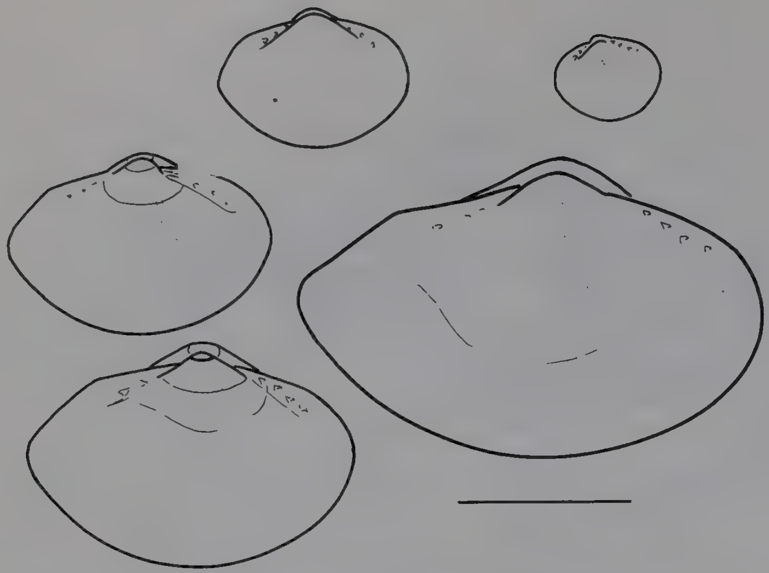

Fig. 40 *Ledella sandersi*: Growth series of shells from Station 191 in lateral outline to show change in shape with increasing size. (Scale = 1 mm).

the rostrum more pointed. The hinge plate and number of teeth are similar in the two species but *L. lusitanensis* has a stronger hinge and the lower edge of the hinge plate curves more sharply towards the internal ligament. When the population variations in *L. sublevis* are taken into account this difference is less obvious.

DISTRIBUTION. Eastern Atlantic.

DEPTH RANGE. 1624–1995 m.

Ledella sandersi new species

HOLOTYPE. BM(NH) 1988090; 5 Paratypes: BM(NH) 1988091

TYPE LOCALITY. Atlantis II Sta. 191, 23°05′S, 12°31.5′E, 1546–1559 m.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		ANGOLA BASIN					
Atlantis II 42	191	2546–2559	14	23°05′S	12°31.5′E	ES	17. 5.68
	192	2117–2154	2	23°02′S	12°19.0′E	ES	17. 5.68
	194	2864	1	22°54′S	11°55′E	ES	17. 5.68

This species is very closely related to *L. verdiensis* (p. 000). The main differences are that the shell is smaller, wider and deeper, with the umbo slightly more central in position. The gills and palps are longer and larger and the foot is small.

DESCRIPTION (Figs 38 & 40). Shell moderately elongate, equilateral or almost so, rostrum blunt, fine concentric sculpture; umbos large, raised, directed medially; antero-dorsal margin straight or almost so, slopes gently to anterior limit of hinge plate where it makes a small angle with rounded anterior margin, postero-dorsal margin also straight or almost so, slopes gently to posterior limit of hinge plate where it makes a marked angle with dorsal margin of rostrum, the edge of which is also straight or almost so, posterior ventral margin not sinuous except in larger specimens which are faintly sinuous, broad, oblique, somewhat raised rostral ridge, shell margin anterior and posterior to umbos raised and slightly sulcate at base of raised part; anterior and posterior hinge plates angular, distally broad but narrow below umbos with relatively few, broad, chevron-shaped teeth, 6 or 7 on each plate; ligament internal, amphidetic, with a small, narrow posterior external part.

Larval shell length 265–285 µm, maximum recorded shell length 3.96 mm.

MORPHOLOGY. The morphology is very similar to *L. verdiensis* and differs only in the relative size of the various organs (Fig. 39). The adductor muscles are large and oval, the anterior slightly larger than the posterior and the inner mantle fold is broad with well developed musculature. The combined siphons are broad and elongate but the ventral margin is not fused nor the junction between the inhalent and exhalent part.

The gills are relatively long extending half across the body, individual gill plates are thick and are approximately 12 in number. The palps are small with approximately 9 folds, the palp proboscides are elongate and narrow. The foot is small and relatively short. The mouth is set far posterior to the anterior adductor muscle, with the oesophagus forming an anteriorly directed semicircle before joining the large stomach. The hind gut makes a single loop to the right side of the body. The visceral and cerebral ganglia are both stout and cylindrical.

DISTRIBUTION. Lower slope depths off Angola.

DEPTH RANGE. 1546–2154 m.

Ledella similis new species

HOLOTYPE. BM(NH) 1988092

TYPE LOCALITY. Sarsia Sta. 63, 46°17.5′N, 4°45.2′W, 1336 m.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		WEST EUROPEAN BASIN					
Sarsia	S.63	1336	8	46°17.5′N	4°45.2′W	ED	24. 7.67

Although the umbos are larger, this species, at first sight, and in external view can be mistaken for *Ledella oxira* (p. 148) or *Ledella parva* (p. 165), however there is a marked difference in hind gut configuration and there are fewer hinge teeth.

DESCRIPTION (Figs 41a, b & c). Shell inequilateral, laterally compressed, elongate-oval in outline with small, blunt posterior rostrum, pattern of light and dark banding, ornament very fine lines of growth; umbos posterior, raised, posteriorly directed; dorsal margin convex, elongate antero-dorsal margin curves almost evenly to narrow anterior margin, postero-dorsal margin slopes first gradually then more steeply to form the dorsal margin of the rostrum, posterior ventral margin with short sinuosity, ventral margin moderately convex; inconspicuous ridge from umbo to tip of rostrum; anterior hinge plate moderately long, broad distally, narrow below umbo, with relatively straight ventral edge, 10 teeth, proximal teeth very small, posterior hinge plate short, ventral edge

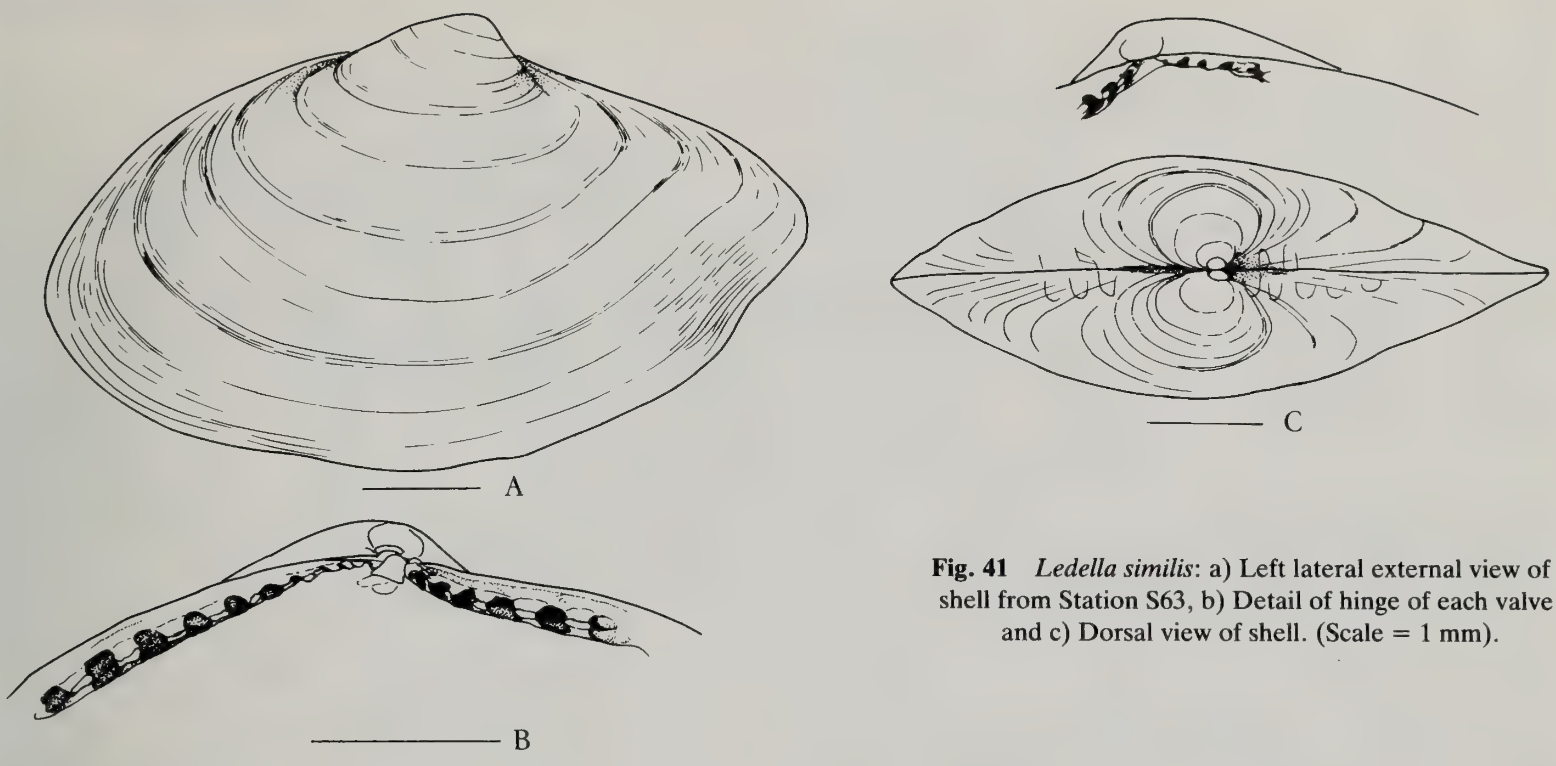

Fig. 41 *Ledella similis*: a) Left lateral external view of a shell from Station S63, b) Detail of hinge of each valve; and c) Dorsal view of shell. (Scale = 1 mm).

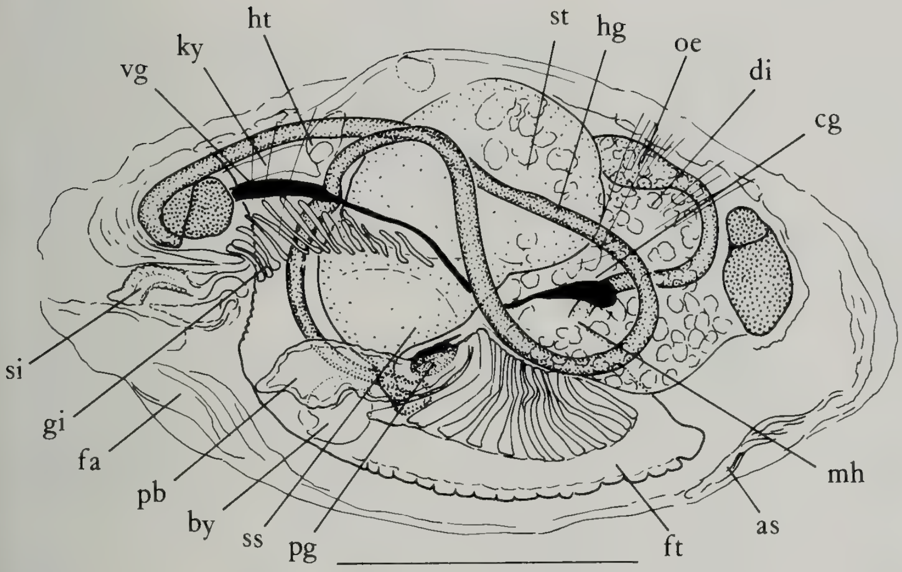

Fig. 42 *Ledella similis*: Lateral view of specimen from the right side with the shell removed to show the arrangement of the body organs. (Scale = 1 mm).

curved, relatively few (6–7) broad chevron-shaped teeth; ligament amphidetic, short, extending below hinge plate with external part consisting of small narrow section posterior to umbo and longer section anterior to umbo.

Larval shell length 210 μm, maximum recorded shell length 6.08 mm.

MEASUREMENTS. Because of the limited number of animals available, shell measurements (mm) were limited to two intact specimens and one opened specimen:-

Length	Height	Width	H/L	W/L	P/Umbo/Total	Teeth (Ant/Post)
4.78	2.91	1.70	0.61	0.34	0.45	
6.08	3.57	2.21	0.59	0.36	0.48	
4.02	2.42		0.60		0.43	10/7

Internal Morphology:

Of the eight specimens, three were decalcified and stained as whole mounts (Fig. 42). The mantle differs little from those species already described. A pair of lateral central ridges between inhalent and exhalent parts of the siphon may function to separate the exhalent and inhalent currents. The tentacle arises from a shallow pocket on either the left or right side at the base of the siphonal embayment. The feeding aperture is well developed, as is the anterior sense organ ventral to the anterior adductor muscle. The adductor muscles differ in size; the anterior being the larger and crescent-shaped. The posterior muscle is more rounded.

The foot is large, with a large, spherical 'byssal' gland and a small posteriorly extended heel. The gills are well developed with approximately 23 filaments. The labial palps are moderately large with 11 broad ridges. The palp proboscides are large and much folded in the contracted state.

The mouth is not far removed from the anterior adductor muscle. The stomach and style sac are large and lie diagonally within the body, the latter penetrating deep into the foot. From the style sac the course of the hind gut is just ventral to the pedal ganglia and then parallels the style sac, posterior to the stomach to the dorsal margin from where it forms a single loop on the right side of the body, which lies short of the anterior adductor muscle. The cerebral ganglia are relatively small, while the pedal ganglia lie central in the foot.

Although the three stained specimens, measure between 4.02–6.08 mm in length (making this one of the larger species of *Ledella*), there were no signs of gonads.

DISTRIBUTION. Bay of Biscay, 1336 m.

Ledella verdiensis (new species)

HOLOTYPE. BM(NH) 1988093

TYPE LOCALITY. Discovery Sta. 8528 No. 1, 17°38′N, 18°35′W, 3150–3155 m.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		CAPE VERDE BASIN					
Discovery	8528	3150–3155	9	17°38′N	18°35′W	WS	2. 7.74

DESCRIPTION (Fig. 43). Shell, inequilateral, elongate oval, rostrate, moderately compressed, strong concentric ridges becoming wider ventrally; umbos large, raised, anterior to midline, directed medially; antero-dorsal margin moderately convex, slopes to form continuous curve with anterior and the ventral margin, postero-dorsal proximal margin straight, moderate slope to posterior limit of hinge plate where it makes an angle to dorsal margin of rostrum, postero-ventral margin very slightly sinuous; anterior and posterior hinge plates elongate, distally broad, proximally narrow below umbo, teeth stout, broad, chevron-shaped 10–12 in anterior series, 8–10 in posterior, number depending on size of shell; ligament internal, amphidetic, triangular, relatively small; pallial sinus deep.

Larval shell length 295 µm, maximum recorded shell length 4.74 mm.

As the size of the shell increases so, to some degree, does the proportionate length of the rostrum compared with total length, consequently there is a small, relative, anterior shift in the position of the umbos.

MORPHOLOGY. The morphology is similar to other species described above (Fig. 44). The adductor muscles are approximately equal in size and oval in cross section. There is a minimal amount of mantle fusion. The siphon is not fused along its ventral margin, nor is it formed into separate inhalent and exhalent parts. However, there is an internal lateral median, longitudinal siphonal ridge on each side, which in life probably separates the inhalent and exhalent parts as well as acting as a guide during the voiding of the faecal rods. There is also a well developed feeding aperture similar to that described for *L. pustulosa* formed by the extension and apposition of the inner and outer mantle lobes. A siphonal tentacle is attached on the right side in the depth of the siphonal embayment. The anterior sense organ is well developed and far anterior in position.

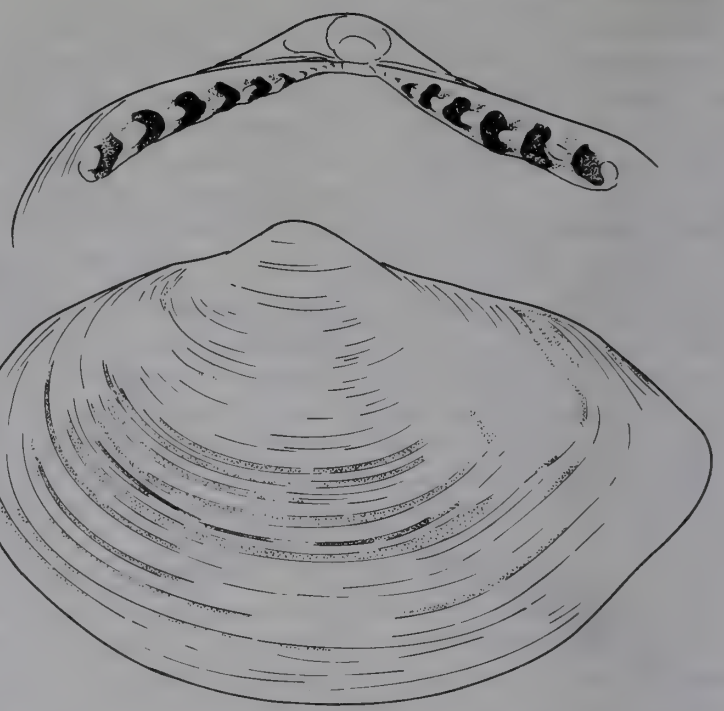

Fig. 43 *Ledella verdiensis*: Left lateral external view of a shell from Discovery Station 8528 and detail of hinge plate of the right valve. (Scale = 1 mm).

The gill axis is relatively short and for the most part lies posterior to the body. The gill plates are small and number 14–16. The palps are very small with few ridges but an extremely long thin palp proboscis is present. The foot is elongate, slender and anteriorly directed, the halves of the divided sole are slender. The ‘byssal’ gland is small while the pedal ganglia are large, elongate and each with a well developed statocyst dorsal to it. The visceral and cerebral ganglia are moderately large.

The mouth is situated somewhat posterior to the anterior adductor muscle. The wide oesophagus enters high on the anterior dorsal face of the large stomach. The style sac is short. The hind gut, after penetrating deep into the foot, forms one loop on the right side of the body. The digestive diverticula lie for the most part anterior to the stomach, with one portion to the right and a larger portion to the left of the body. Part of the latter differs in appearance from the remainder, the tubules being somewhat larger and slightly lighter in colour compared with the others. This distinction has been observed in other nuculanids (p. 129) and probably reflects a division of function. Differences similar to those described for *N. minuta*, occur in the digestive ducts that serve the three portions of the digestive diverticula. The kidney is somewhat enlarged and extends anteriorly into the body to the right side of the stomach.

DISTRIBUTION. Abyssal depths off the Cape Verde Islands, 3150–3155 m.

Ledella oxira (Dall, 1927)

HOLOTYPE. USNM No. 108190.

TYPE LOCALITY. Off Southeast coast of United States (Lat. 30°58′N, Long. 79°38′W), 678 m.

SYNONYMY. *Leda oxira* Dall 1927 *Proc. U.S. natn. Acad. 70*, art. 18, p. 8, 9.
Ledella oxira Johnson 1934 *Proc. Boston Soc. 40*, p. 16.

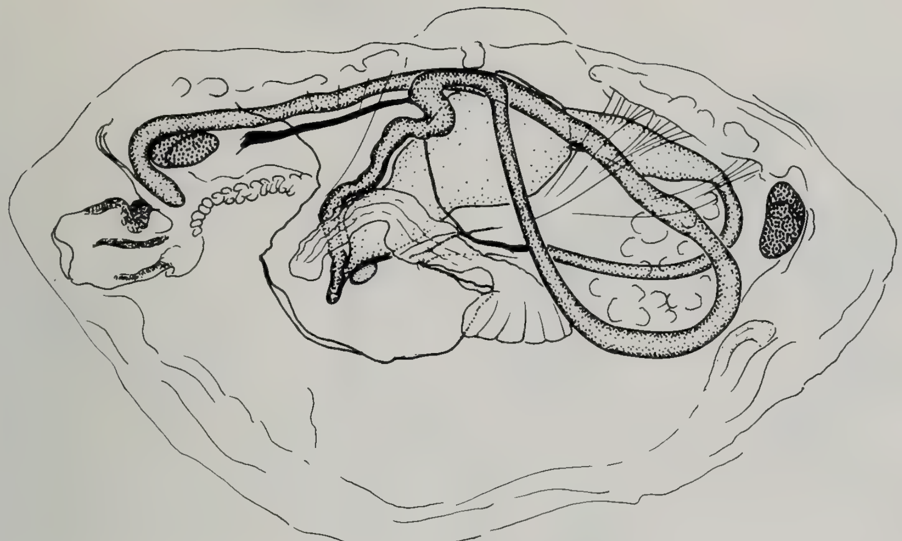

Fig. 44 *Ledella verdiensis*: Lateral view of a specimen from the right side with the shell removed to show the arrangement of the body organs. (Scale = 1 mm). For identification of parts see Fig. 42.

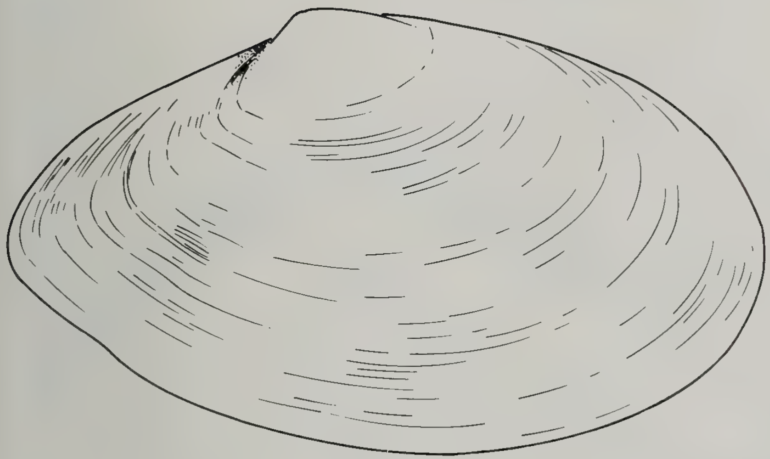

Fig. 45 *Ledella oxira*: Right lateral external view of shell from Station 167. (Scale = 1 mm).

MATERIAL. USNM No. 108190.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			BRAZIL BASIN				
Atlantis II 31	162	1493	1	8°02.0′S –7°56.0′S	34°03.0′W –34°09.0′W	ES	19. 2.67
	167	943–1007	2	7°58.0′S –7°50.0′S	34°17.0′W	ES	20. 2.67

This species resembles both *Ledella parva* and *Ledella semen* in its shell characters. Nevertheless, the anatomy of *L. oxira*, and the course of the hind gut in particular, differs markedly from *L. parva*. The possible synonymy with *L. semen* is discussed later. (p. 166).

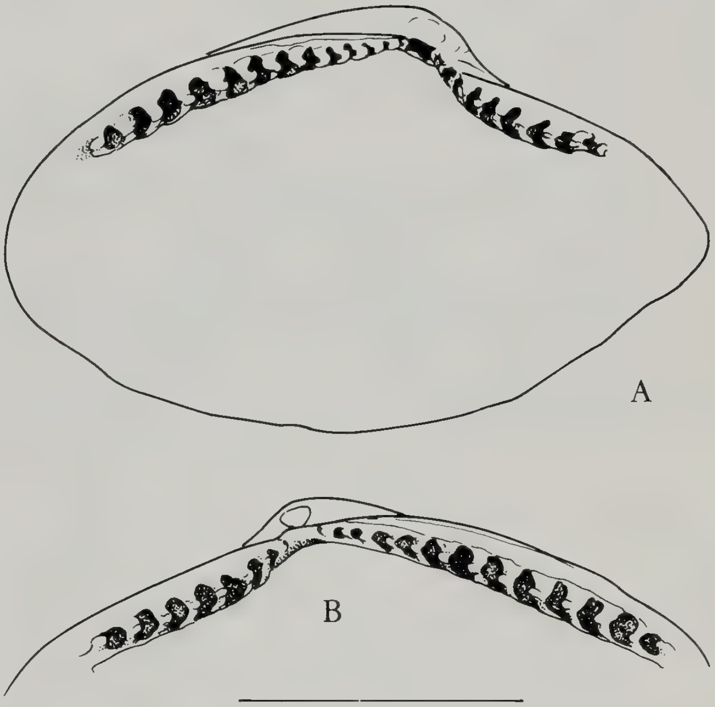

Fig. 46 *Ledella oxira*: (a) Lateral internal view of right valve of the holotype specimen (USNM No. 108190); (b) hinge plate detail of left valve from Station 167. (Scale = 1 mm).

DESCRIPTION (Fig. 45 & 46a & b). Shell inequilateral, elongate-oval, laterally compressed, moderately strong, surface smooth with fine lines of growth; short, blunt umbo far posterior, slightly raised, somewhat posteriorly inclined; anterior and posterior dorsal margin moderately convex, antero-dorsal margin forms long smooth curve with anterior margin, short postero-dorsal margin proximally straight, or almost so, slopes gradually to posterior edge of hinge plate, thereafter more acutely to form dorsal margin of short rostrum, postero-ventral margin slightly sinuous, ventral margin long, smooth and moderately convex; small inconspicuous ridge from umbo to tip of rostrum; hinge plate moderately strong, relatively broad, narrower below umbo, anterior hinge plate long, ventral edge relatively straight, 13 teeth, posterior hinge short, ventral edge curved towards umbo, 8 teeth; ligament amphidetic, relatively elongate, does not extend ventral to hinge plate.

MEASUREMENTS (mm).

Length	Height	Width	H/L	W/L	P. umbo/TL	Teeth Ant./Post.
3.12	1.80		0.58		0.38	13/8
1.74	1.09	0.62	0.62	0.35	0.40	

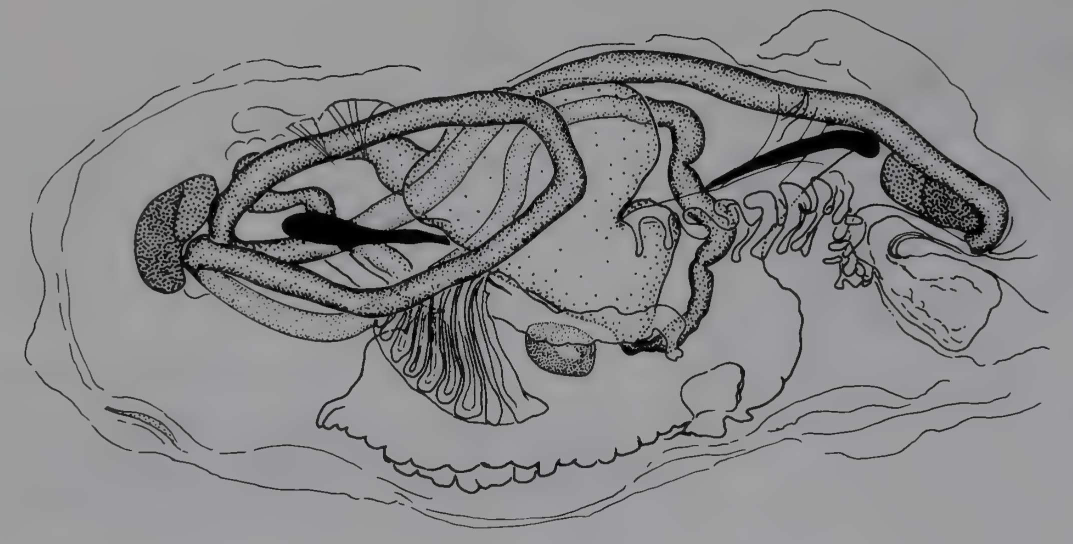

Fig. 47 *Ledella oxira*: Lateral view of a specimen from the left side with the shell removed to show the arrangement of body organs. For identification of parts see Fig. 42. (Scale = 1 mm).

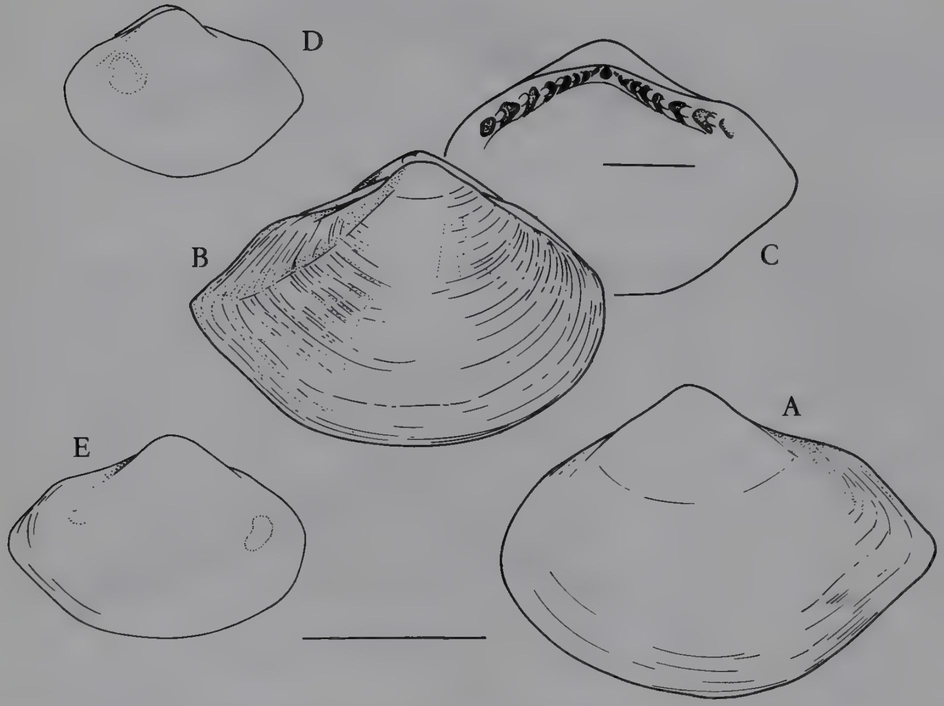

Fig. 48 *Ledella galatheae*: a) Left lateral external view of holotype, b) right lateral external view of specimen from Biogas VI Station DS 78, c) right lateral internal view of specimen from Station 287, d) and e) lateral external views of shells in outline from Station 287. (Scales = 1 mm; a, b, d & e drawn to same scale).

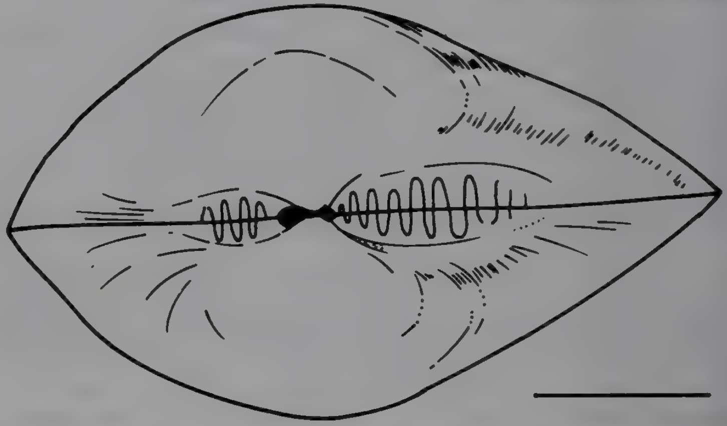

Fig. 49 *Ledella galatheae*: Dorsal view of specimen from Station 287. (Scale = 1 mm).

MORPHOLOGY. As there were only three specimens available, the description of the internal morphology is based on one whole mount stained in haemotoxylin (Fig. 47).

The mantle structures differ little from those described for *L. pustulosa*. The siphonal tentacle originates on the right side close to the base of the combined siphon. The adductor muscles are approximately equal in size and oval in shape; the long axes of the muscles are parallel to the shell margins.

The foot is moderately large with a large byssal gland. The nervous system is well developed with a large pedal ganglion, situated in the anterior half of the neck of the foot. The cerebral and visceral ganglia are large and club-shaped. The gills have approximately 15 pairs of alternating plates. The palps are small with 8 broad ridges while the palp proboscides are slender although much contracted in the preserved specimens. (Fig. 47).

The stomach and style sac are relatively large. The hind gut extends only a short distance into the foot before turning dorsally, posterior to the stomach. At the posterior dorsal margin of the body its course is to the right side of the body as far as the inner face of anterior adductor muscle where it crosses to the left side to form one loop before returning to the right again at the inner face of the anterior adductor. From there its course is dorsal to the anus. This configuration is but the elongation of the single-looped primitive condition

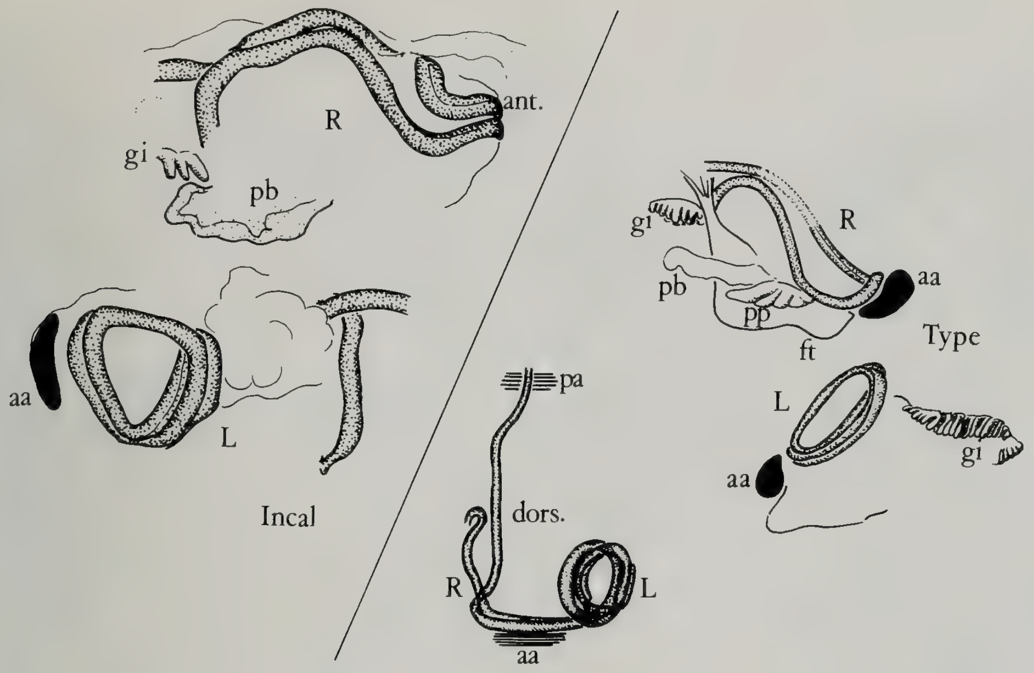

Fig. 50 *Ledella galatheae*: Comparative views of the hind gut of the type specimen (A) and the specimen from Station Incal WS03 (B).

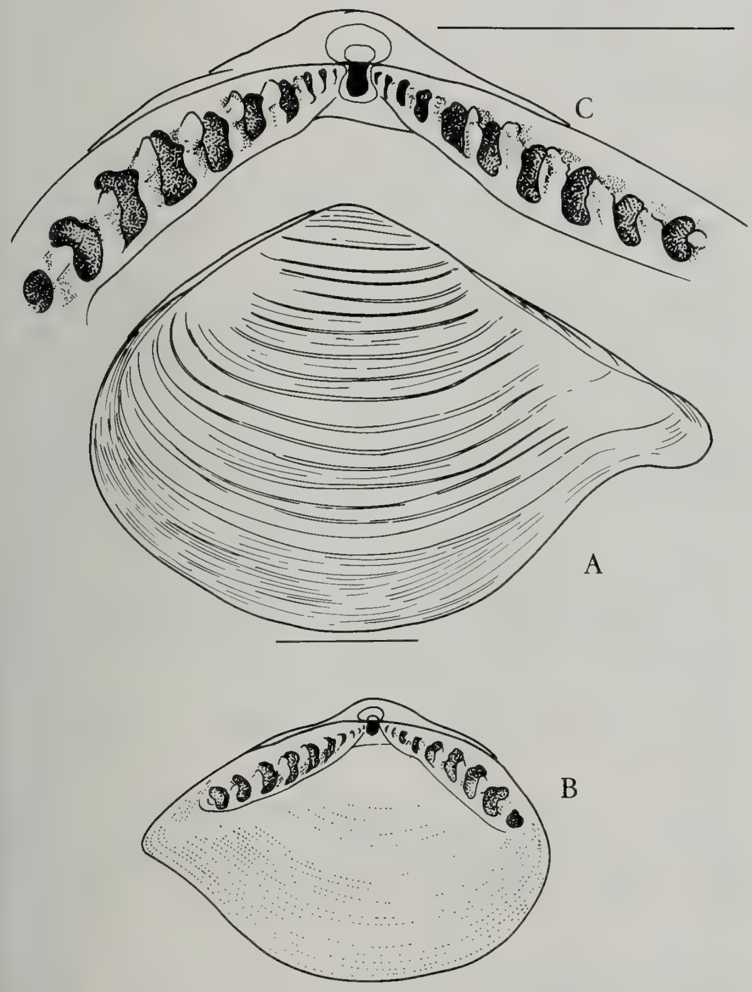

Fig. 51 *Ledella solidula*: (a) Left lateral external view of a specimen from Station 293. Note this is a large specimen with a thickened and internal ventral margin and therefore somewhat atypical (see Fig. 55); (b) left lateral internal view of a specimen from Station 118; (c) hinge of latter specimen in greater detail. (Scale = 1 mm).

which, by virtue of the space between adductor and mouth and oesophagus is able to extend to the left side of the body. Although this is a way of accommodating the lengthened hind gut it is not a common condition in deep sea protobranchs and it has been only recorded in a few other deep-sea species, notably *Yoldiella curta* Verrill & Bush (Allen, Hannah & Sanders, in m/s).

DISTRIBUTION. Off coast of South America and southeast coast of U.S.A, 673–1493 m.

Ledella galatheae Knudsen 1970

HOLOTYPE. ZMUC

TYPE LOCALITY. 'Galathea' Sta. 30, 0°42′N, 5°59′W, 5160 m, off W. Africa.

MATERIAL. Holotype specimen.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
GUINEA BASIN							
Walda	DS31	4279	1	3°17.5′N	2°01.7′W	ES	
SIERRA LEONE BASIN							
Knorr 25	287	4934–4980	41	13°12.0′N	54°53.8′W	ES	25. 2.72
WEST EUROPEAN BASIN							
Jean Charcot (Biogas VI)	DS78	4706	1	46°31.2′N	10°23.8′W	ES	25.10.74
	DS81	4715	1	46°28.3′N	10°24.6′W	ES	27.10.74
(Incal)	WS03	4829	1	48°19.2′N –48°19.1′N	15°23.3′W –15°22.5′W	WS	1. 8.76

Despite earlier doubts about the identity of the above specimens (see below), comparison with the original type material leaves no doubt that the specimens in our collections are *Ledella galathea*.

DESCRIPTION (Figs. 48 & 49). The original shell description (Knudsen, 1970) is accurate and does not require modification, however, we found ourselves at something of a loss when we compared the anatomy of the above specimens against the original description. The internal morphology of the present specimens does not even closely resemble the description given by Knudsen (1970). The original description indicates a primitive gut morphology with a single hind gut loop to the right side of the body. In addition Knudsen (1970)

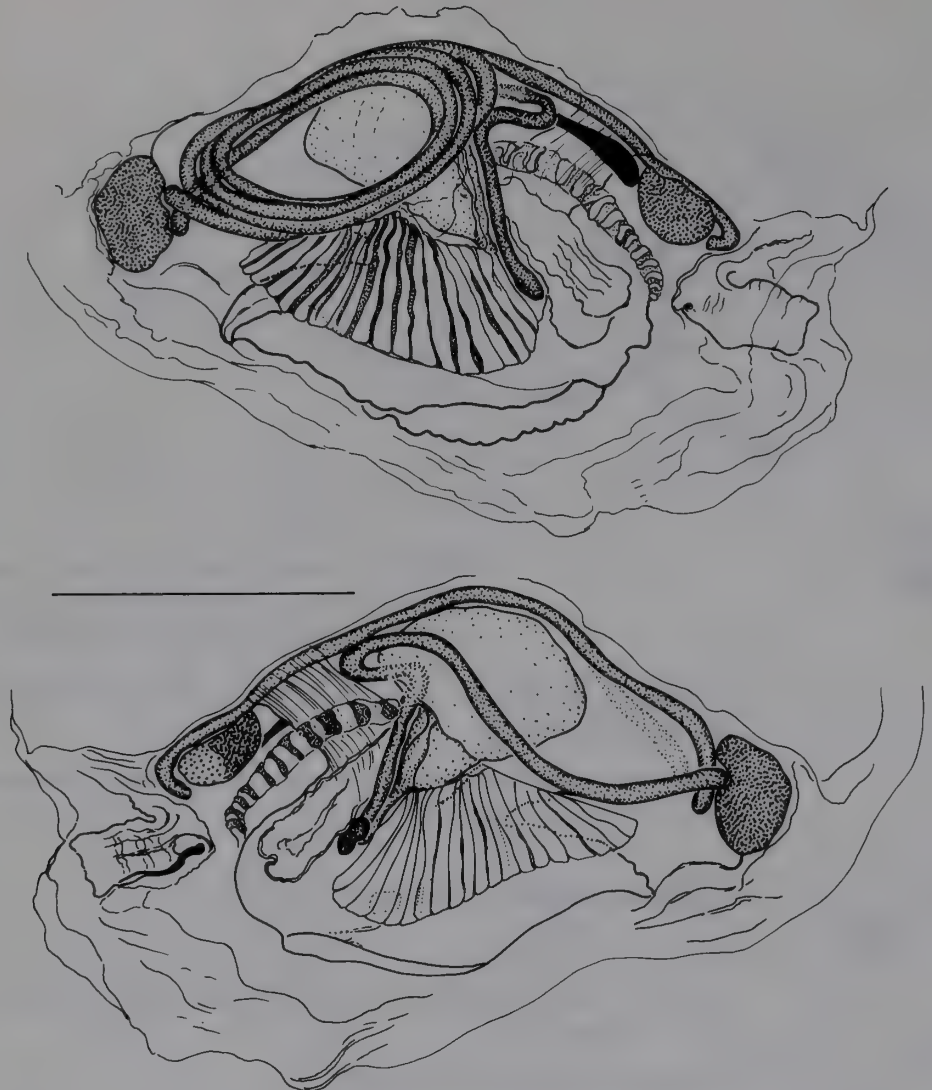

Fig. 52 *Ledella solidula*: Lateral views of a specimen from the left and right sides with shell removed to show the arrangement of the body organs. (Scale = 0.5 mm).

refers to a finely 'serrate' mantle edge at the margin of siphonal embayment. Although we have been constrained by the state of the preservation of our specimens it is clear that their morphology is similar to that of *Ledella acuminata* and *L. solidula* (Figs. 52 & 53). Thus, the hind gut passes from the right to left side of the body and forms four coils on the left side (Fig. 50). Fortunately on examination of the type specimen we found sufficient body remains to show that the anatomy of the Galathea material was the same as that of the present specimens i.e. with multiple coils on the left side. Another notable morphological character is the small size of the palp. We can only conclude that either there was an accidental transposition of a soft part drawing in the Galathea Report or that the shell relating to the body drawn by Knudsen 1970 (his figure 14c & d) was not an example of this species. This would not be at all surprising to us considering the great difficulties there are in distinguishing the younger specimens of the less common species of the subfamily from each other.

Ledella solidula (Smith 1885)

HOLOTYPE. BM(NH) 1887.2.9.2940.

TYPE LOCATION. Station 120, Challenger Expedition, off Pernambuco, 1234 m.

SYNONYMY. *Leda solidula* Smith 1885 *Chall. Rep. Lam.* p. 233, pl. 19, Fig. 6, 6a.

Nucula solidula (Smith): Aquayo & Jaume, 1950. *Catalogo Muluscos de Cuba, III, Scaphopoda, Pelecypoda*, p. 644.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			NORTH AMERICA BASIN				
Atlantis II 24	118	1537–1830	184+ 247V	32°19.4′N –32°19.0′N	64°34.9′W –64°34.8′W	ES	18. 9.66
			GUIANA BASIN				
Knorr 25	293	1456–1518	4	8°58.0′N	54°04.3′W	ES	27. 2.72

Dall (1886) records valves from Cape San Antonio (1833 m) and from the Yucatan Strait (1170 m), while James (1972) also records shells from the North East Gulf of Mexico in 1000 m and between 1097–1189 m. Shallow water records by Fischer-Piette (1973) from Calypso Stations 48 & 88 at depths of 40 m and 39 m respectively must be suspect.

DESCRIPTION (Figs. 51a, b & c). Shell ovate-triangular, moderately strong, moderately inflated, rostrum extended, regular, broad, concentric ridges, approximately equilateral; umbo, slightly raised, beaks medially directed, position changes with increasing size; dorsal margin convex, antero-

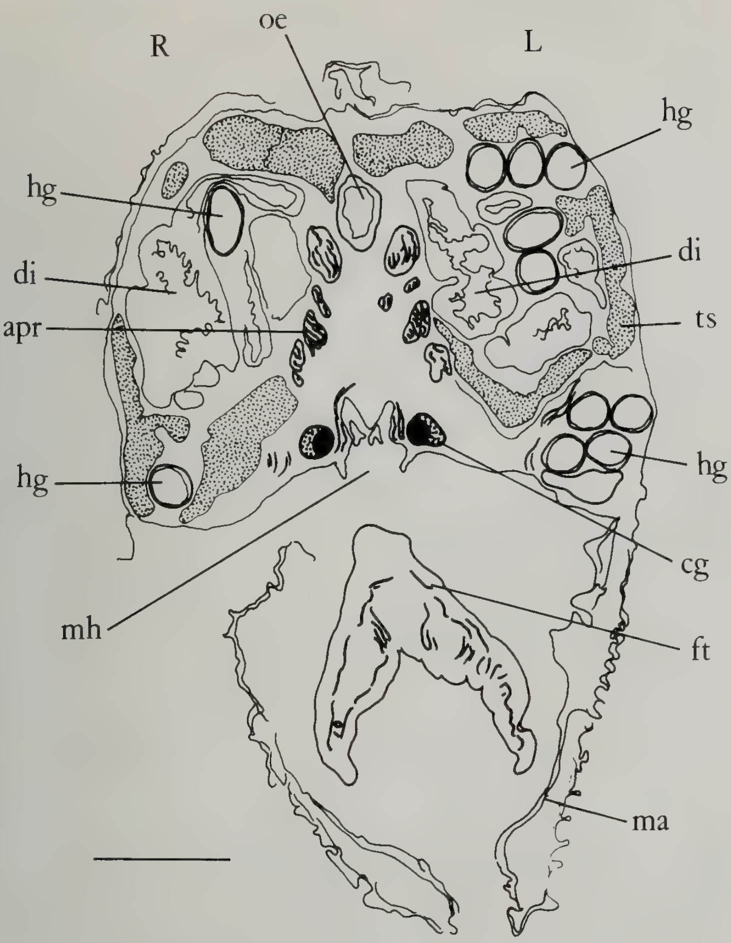

Fig. 53 *Ledella solidula*: Transverse ventral section of body immediately anterior to the stomach. (Scale = 0.1 mm).

dorsal margin slopes sharply to form curve with anterior edge, postero-dorsal margin slopes more gradually from umbo, margin almost straight in large specimens but usually slightly convex, angled slightly at distal end of hinge plate, keel extends from umbo to tip of sharp pointed rostrum with concentric ridges making a right angle at its crest, postero-ventral margin conspicuously sinuous, ventral margin long, moderately convex; hinge plate broad, strong, relatively long, anterior and posterior parts with approximately nine chevron-shaped teeth (number varies with length), six distal teeth are large and strong, proximal teeth progressively smaller; ligament amphidetic, internal, goblet-shaped; adductor muscle scars visible.

Larval shell length 245 µm, maximum recorded length 5.78 mm.

MORPHOLOGY. Although similar to *L. galathea*, the organization of the hind gut differs from the others previously described. In other details the morphology is similar to other species described above. (Fig. 52).

The anterior bean-shaped adductor muscle is approximately twice the size of the oval posterior muscle. The gills are moderately small, with up to 12 plates in each demibranch. The labial palps are relatively large with 14–24 ridges and, as in the case of the gill plates, the number being dependent on the size of the individual. The palp proboscides are long and moderately thin.

The foot is large with a small 'byssal' gland. The pedal ganglion is large while the cerebral and visceral ganglia are long and thin and moderate in size.

The stomach lies anterior in the body. The style sac penetrates the lower half of the foot posterior to the pedal ganglia. The hind gut extends further into the foot to a point immediately dorsal to the byssal gland. From there it curves back on itself posterior to the stomach to the dorsal body margin where it passes the right side. From there it takes an anterior course to the anterior adductor muscle where it crosses to the left side to form four coils (Fig. 53). These lie in the anterior half of the body between the anterior adductor muscle and a line vertical to the umbo. After forming the coils the hind gut returns to the right side again, immediately posterior to the anterior adductor, and from there dorsally to the anus.

One male specimen (4.8 mm total length) from Station 293 was found to be in the process of releasing sperm. These were present in the mantle cavity, on the gills and within the siphon. The volume of body occupied by the testis was estimated at 17.0%.

The change in shell shape with growth is particularly marked in this species (Figs. 54 & 55). In the largest specimens there is a slight change in the direction of growth at the ventral edge (Fig. 51) although this is to a much lesser extent than that described in the case of *L. ultima* (p. 161). With increasing length, the rostrum becomes more elongate and may be pointed and the dorsal margin becomes more convex.

A large number of dead shells were present in the sample from Station 118 and the length of these were compared with those of live specimens (Fig. 56). In the case of valves only one was recorded in the case of those joined by hinge and ligament and only half of the total for each size of the single valves (+ 1 in case of an odd number). From this it is clear that the vast majority of dead shells are at the maximum size of the species with few at lengths below 2 mm which would appear to support the contention that mortality patterns in deep sea bivalves differs markedly from those in shallow waters where the greatest mortality occurs in juveniles (see Oliver & Allen 1980).

DISTRIBUTION. Surinam Basin, Gulf of Mexico and Bermuda Slope from 1000–1830 m.

Ledella acuminata (Jeffreys 1870)

LECTOTYPE. USNM No. 199672.

TYPE LOCALITY. Mediterranean 550 metres.

SYNONYMY. *Leda acuminata* Jeffreys 1870 *Ann. Mag. nat. Hist.* Ser. 4, *6*, p. 69.
Leda messanesis Jeffreys 1879 *Proc. zool. Soc. Lond.* 1879, p. 576 (in part).
Yoldiella acuminata Warén 1978 *Sarsia, 63,* p. 215. Figs. 1, 2, 10 & 11.

MATERIAL. Collections from the Porcupine Expedition in the USNM & BMNH have been examined.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
				BAY OF BISCAY			
Sarsia	56	641	1	43°43.0′N	3°47.8′W	ED	19. 7.67
	63	1336	1	46°17.5′N	4°45.2′W	ED	24. 7.67
	66	1427	1	46°16.3′N	4°44.0′W	ED	25. 7.67
Thalassa	Z397	511	2	47°33.8′N	7°12.6′W	GBO	22.10.73
	Z399	825	1	47°34.8′N	7°18.1′W	GBS	22.10.73
	Z400	1175	1	47°33.4′N	7°19.0′W	GBS	22.10.73
	Z413	805	3	48°03.1′N	8°29.4′W	PBS	24.10.73
	Z414	650	7	48°05.0′N	8°29.8′W	PBS	24.10.73

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
	Z415	386	1	48°07.2′N	8°26.2′W	PBS	24.10.73
	Z424	475	2	48°27.9′N	9°44.3′W	PBS	25.10.73
	Z435	1050	1	48°39.7′N	9°53.2′W	PBS	26.10.73
		MEDITERRANEAN					
Atlantis II–59.	211	500–509	90	33°57.0′N	15°08.2′W	ES	2. 9.70

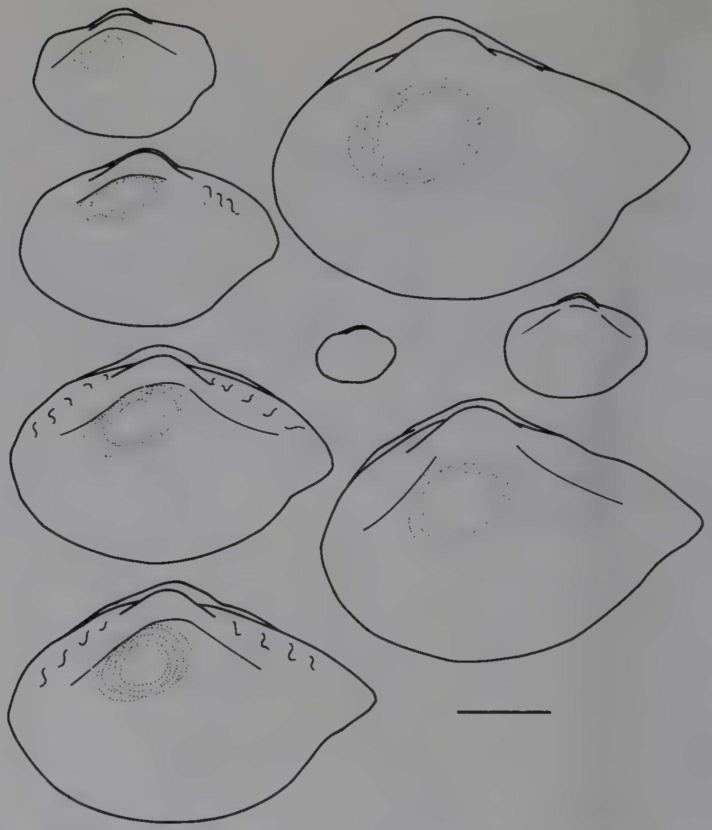

Fig. 55 *Ledella solidula*: Growth series of shells from Station 118 in lateral outline to show change in shape with increasing size. (Scale = 1 mm).

The shell morphology has been well described by Warén (1978) and requires little further addition.

Description (Figs. 57 & 58). Shell thin, elongate-oval with pointed rostrum, ornament of fine, concentric ridges becoming more conspicuous towards ventral margin; dorsal margin weakly convex, antero-dorsal margin, gradual curve, slopes to smooth curve with anterior margin, proximal postero-dorsal margin relatively straight at posterior limit of hinge plate, slope increases to form convex dorsal margin of elongate rostrum, postero-ventral margin sinuous, ventral margin long, moderately smooth curve; umbo usually anterior to mid line, moderately low in profile, medially directed; low rounded keel extends from umbo to top of rostrum, concentric ridges form an approximate right angle at keel; anterior and posterior hinge plates strong, broad, elongate, each with 7–11 chevron-shaped teeth; ligament amphidetic, largely internal, goblet-shaped with small external extensions on either side of umbo; adductor scars visible.

Larval shell length 200 µm, maximum recorded length 4.93 mm.

Morphology. The basic form of the body is similar to that of other species of *Ledella* with a hind gut with a coiled configuration on the left side of the body (Fig. 59).

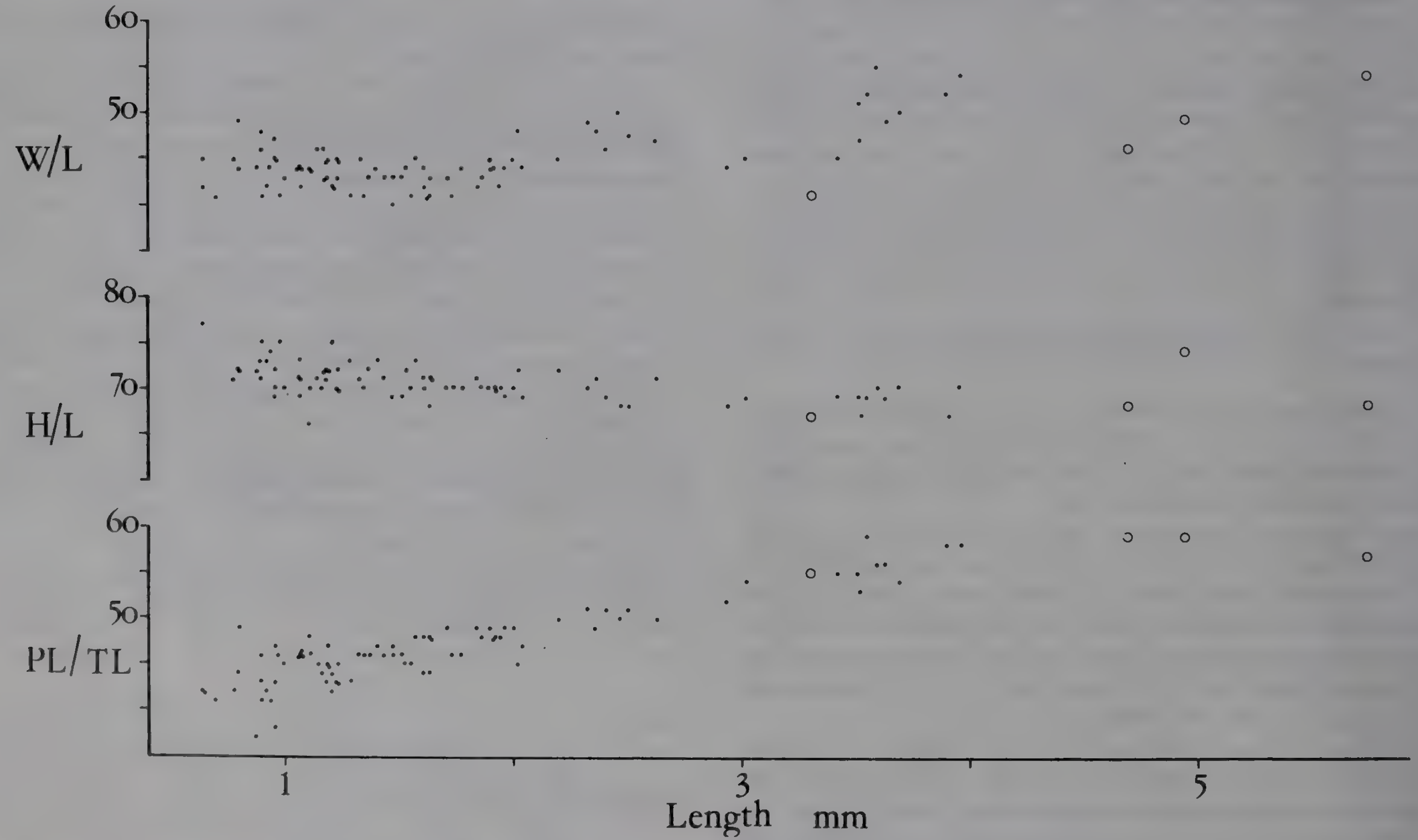

Fig. 54 *Ledella solidula*: An analysis of change in shape with growth as shown by the ratios posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 293 (open circles) and Station 118 (points).

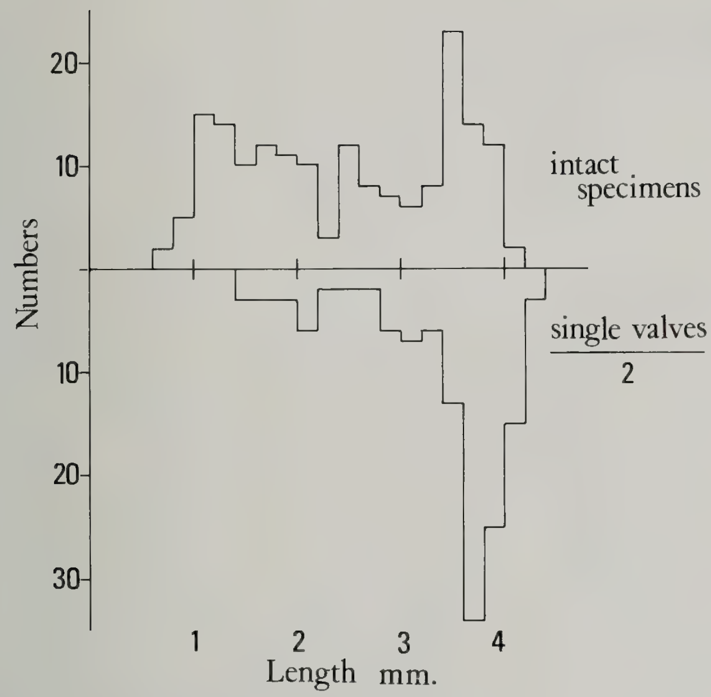

Fig. 56 *Ledella solidula*: Comparative histograms of size range of living and dead shells (see text for further explanation).

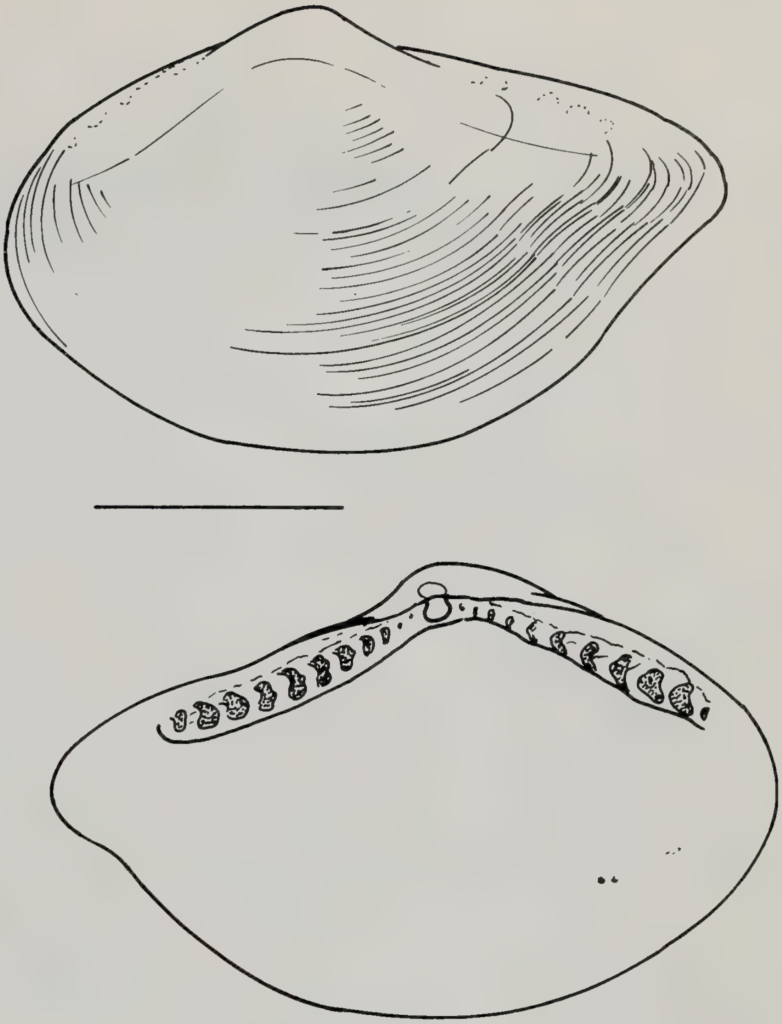

Fig. 57 *Ledella acuminata*: Left lateral external view of lectotype (USNM No. 199672) 310 fm. Mediterranean and lateral internal view of lectotype. (Scale = 1 mm).

The adductor muscles differ in size and shape. The anterior muscle is 2 or 3 times the size of the posterior, it is bean-shaped with the longitudinal axis parallel to the anterior margin. The posterior adductor is elongate-oval in shape with the longitudinal axis parallel to the dorsal margin. The siphon is moderately large and muscular with the siphonal tentacle usually inserted to the right at the base of the siphon. The feeding aperture is well developed.

The species has the greatest number of labial palp ridges of any species described here (22–28 depending on the size of the animal), however, the area of body covered by the palps is similar to that of most other species. The palp proboscides are large, long and in the contracted state, much folded. The gills are moderately well developed with 22–26 filaments. Posterior of the foot the inner demibranchs lie in close proximity to one another, those close to the base of the siphon appear to be interlocked.

The foot is large, peripherally deeply papillate and with an extended heel. The 'byssal' gland is large. The pedal retractor muscles are similar to those described for *L. pustulosa*. The cerebral and visceral ganglia are relatively small and cylindrical in shape while the pedal ganglia are large.

The stomach and style sac are large. The hind gut follows a course similar to that described for *L. solidula* with a single loop to the right and four or five coils to the left of the body. The number of coils immediately visible through the transluscent shell varies from 2–5, coils overlain by others often being masked in lateral view (Fig. 60). In a subsample of nine sectioned individuals taken from Station 211 the number of coils varied, 5 specimens having 5 coils, the remaining 4 with 4 coils. The outline shape of the coils is variable. Hind gut morphology is very similar to that seen in *Tindariopsis acinula* (Dall): (Sanders & Allen, 1977).

Shell changes shape with increasing length (Fig. 60 & 61). The rostrum becomes increasingly prominent with a corresponding change in the relative position of the umbo, i.e. becoming more anterior with increasing length. The width of the animal relative to total length changes little during growth, but there is a slight but gradual decrease in relative height. (Fig. 61). *L. acuminata* is one of the least inflated species of the genus (Fig. 3f) with an average ratio of width to length of 0.37 (Sta. 211).

In section the smallest specimen with recognizable gonad tissue was 2.3 mm length. The number of eggs varies from 159 in an individual 3.00 mm in length to 587 in an individual 4.6 mm. The maximum length of the eggs was relatively constant in specimens from Station 211 (140–148 μm) although in general the larger the individual the greater the area of body covered by gonad. There is an approximately equal number of males and females (Fig. 62).

DISTRIBUTION. Bay of Biscay and Mediterranean.

DEPTH RANGE. 475–1427 m.

Ledella ultima (Smith 1885)

LECTOTYPE. BM(NH) 1887.2.9.3354; 1 left valve, designated herein, Paralectotypes: 2 right valves. (Holotype *L. bushae* USNM No. 52 156, type locality off Martha's Vineyard about 4700 m. Holotype *L. crassa* Zoological Museum University of Copenhagen (ZMUC), type locality 'Galathea' Sta. 24, off W. Africa, 3°54.0'N, 8°22.0'W, 3196 m.

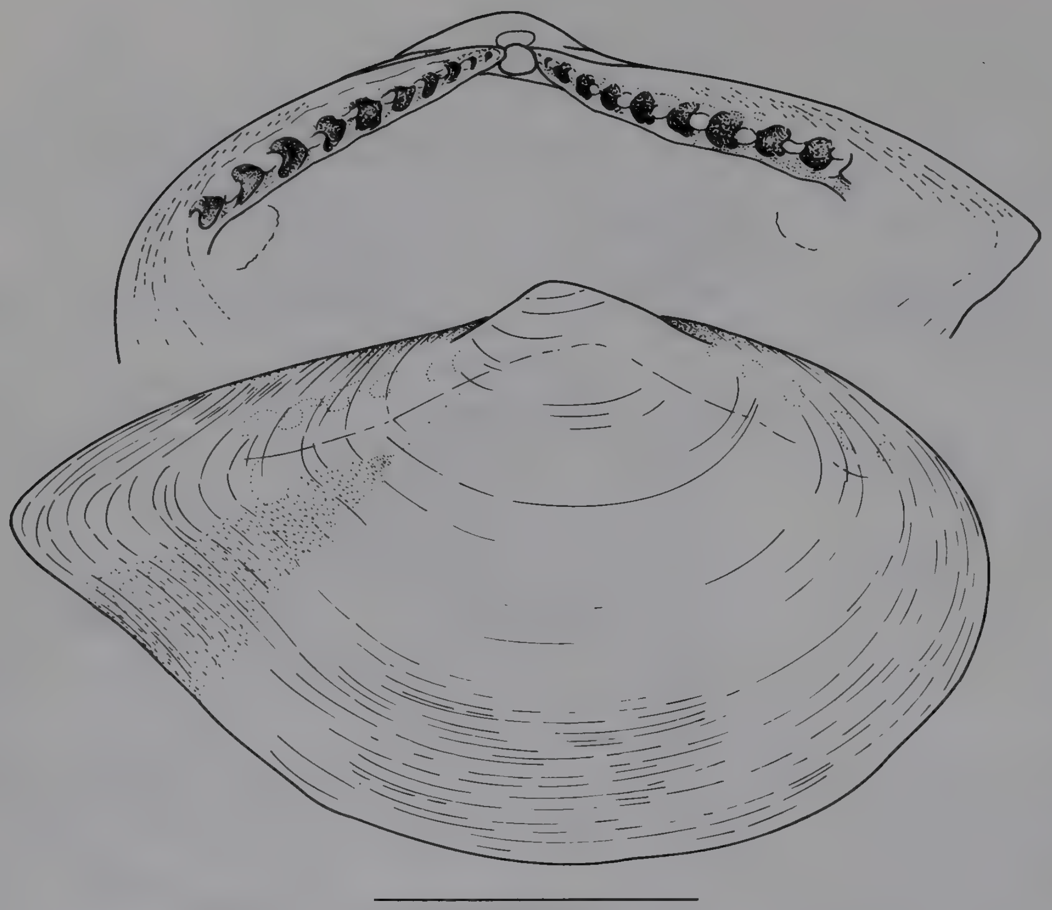

Fig 58 *Ledella acuminata*: Left lateral external view of specimen from Station 211 and lateral internal view of specimen from Station 211 to show detail of hinge plate. (Scale = 1 mm).

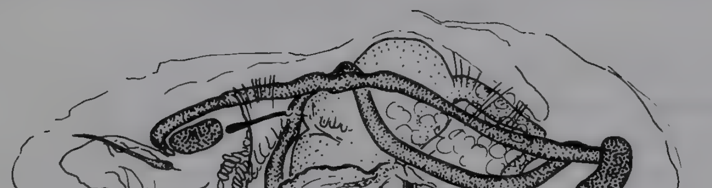

Fig. 59 *Ledella acuminata*: Lateral views of specimen from the left and right sides with the shell removed to show the arrangement of the body organs. For identification of parts see Fig. 42. (Scale = 1 mm).

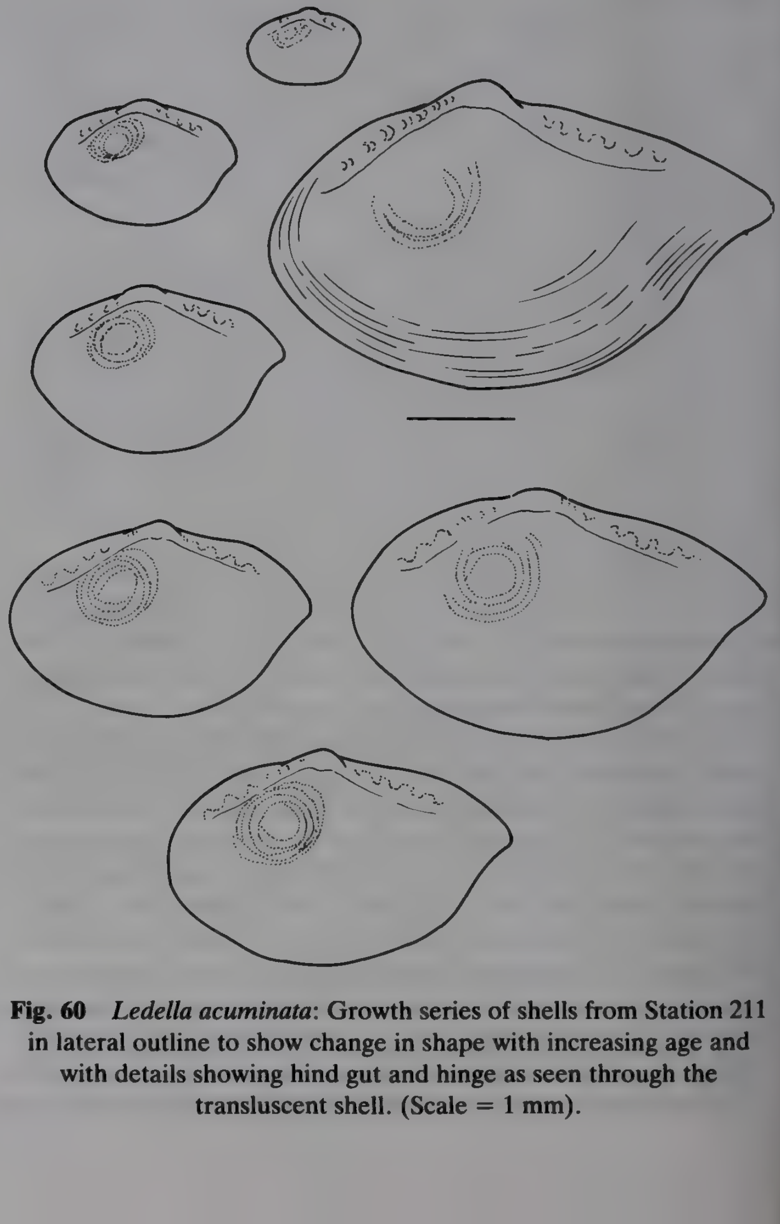

Fig. 60 *Ledella acuminata*: Growth series of shells from Station 211 in lateral outline to show change in shape with increasing age and with details showing hind gut and hinge as seen through the transluscent shell. (Scale = 1 mm).

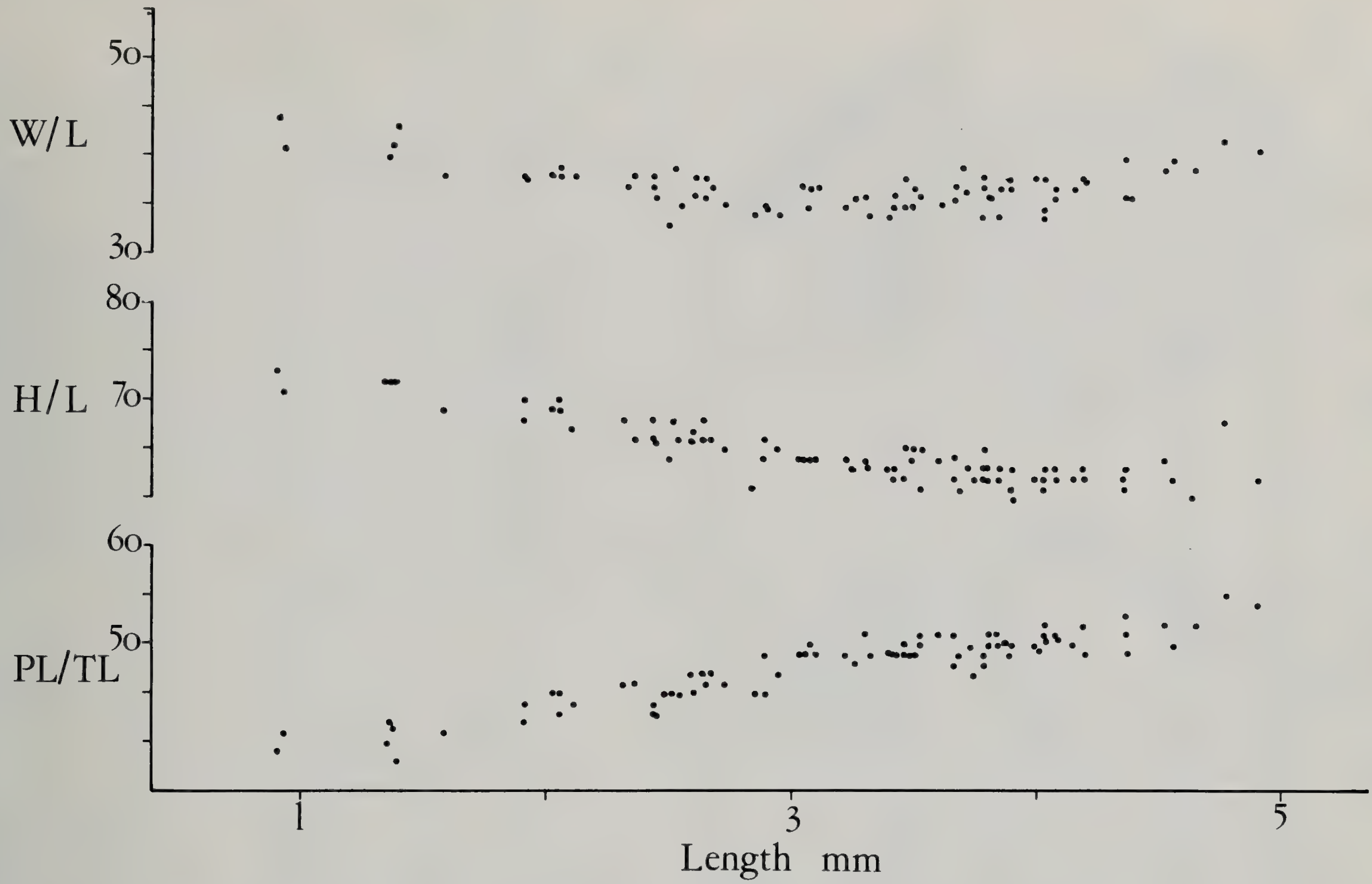

Fig. 61 *Ledella acuminata*: Analysis of change in shape with growth as shown by the ratios posterior umbo length/total length (PL/TL), height/length (H/L), width/length (W/L) plotted against length for specimens from Station 211.

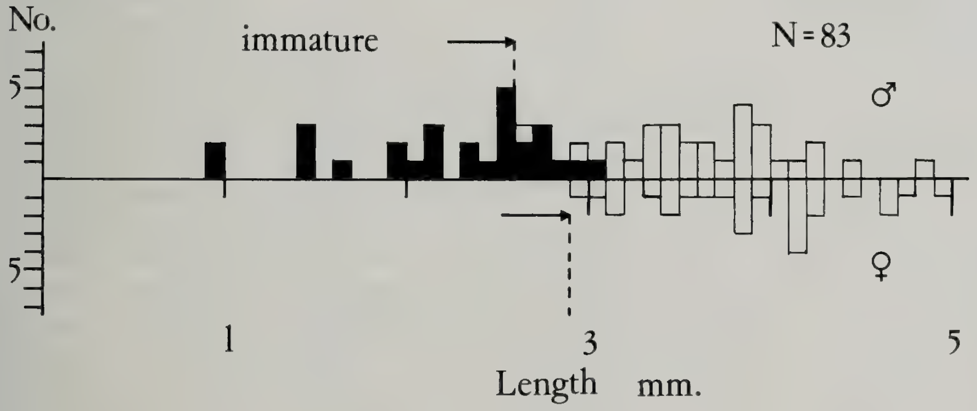

Fig. 62 *Ledella acuminata*: Histogram of specimens from Station 211, identified as immature (solid record) and maturing (open record) males and females as recorded through the transluscent shell.

TYPE LOCALITY. Challenger Sta. 5, 24°20.0′N., 24°28.0′W, 5011 m, Southwest of the Canary Islands.

SYNONYMY. *Leda ultima* Smith, 1885. *Exp. Chall. 13*, p. 324. Figured (no number) on p. 324.
Ledella messanensis Verrill & Bush, 1897. *Am. J. Sci. 54*, Fig. 13, 18 (*non Leda messanensis* Seguenza MS, *in* Jeffreys, 1870).
Nuculana ultima (Smith): Clarke, 1961 *Bull. Mus. Zool. Harv. 125*, p. 375.
Ledella crassa Knudsen, 1970. *Galathea Rep. 11*: pp. 30–32, Fig. 12, 13, pl. 3. Fig. 1.
Ledella bushae Warén, 1978. *Sarsia 63*, p. 213, Figs. 8 & 9.
Ledella bushae Warén: Warén, 1981. *Bull. Zool. Nom. 38*, p. 134–37.

This is the most common species of *Ledella* present in the Atlantic and it has a widespread distribution. There are multiple descriptions of the species under different names.

Our extremely large collections show that *L. ultima* (Smith) from the Canaries (named *L. crassa* by Knudsen (1970)), from the north west Atlantic (named *L. messanensis* by Verrill & Bush (1897, 1898)), and *L. bushae* (named by Warén (1978) and later confirmed as type species following Warén 1981) are one and the same species. Detailed observations from our own material from these and other localities show two points of difference from the earlier descriptions:– (a) the maximum number of teeth is greater than previously recorded (see below) and (b) a thickened ventral edge is present in older specimens particularly, but not exclusively, those collected off West Africa. Both of these differences simply relate to the large numbers in the present collections which extend the size range of the species.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
NORTH AMERICAN BASIN							
Atlantis	111	3742	17	37°59.0′N	69°32.0′W	AD	22. 5.61
264	112	3752	1	38°05.0′N	69°36.0′W	AD	24. 5.61
273	JJ1	4436	14	37°27.0′N	68°41.0′W	AD	2.10.61
	HH2	2488	2	39°26.0′N	70°34.0′W	AD	3.10.61
277	JJ3	4540	19	37°13.1′N	68°39.6′W	AD	25. 6.62
Atlantis II	69	4663	5	36°15.0′N	67°51.0′W	AD	23. 8.64
12	70	4680	1086	36°23.0′N	67°58.0′W	ET	23. 8.64
	73	1330–1470	1	39°46.5′N	70°43.3′W	ET	25. 8.64
Chain	77	3806	1423	38°00.7′N	69°16.0′W	ET	30. 6.65
50	78	3833	250	38°00.8′N	69°18.7′W	ET	30. 6.65
	80	4970	5	34°49.8′N	60°34.0′W	ET	2. 7.65
	81	5042	3	34°41.0′N	66°28.0′W	ET	2. 7.65
	84	4749	702	36°24.4′N	67°56.0′W	ET	4. 7.65
	85	3834	1045	37°59.2′N	69°26.2′W	ET	5. 7.65
Atlantis II	92	4694	209	36°20.0′N	67°56.0′W	ET	13.12.65
17	93	5007	1	34°39.0′N	66°26.0′W	ET	14.12.65
	95	3753	134	38°33.0′N	68°32.0′W	ET	17.12.65
Chain 58	101	4700	321	36°24.2′N	68°01.3′W	ET	3. 5.66
Atlantis II	108	4739	8	00°00.0′N	00°00.0′W	ET	7. 8.66
23	109	4750	554	00°00.0′N	00°00.0′W	ET	8. 8.66
	110	4750	13	00°00.0′N	00°00.0′W	ET	8. 8.66
	112	2900	1	00°00.0′N	00°00.0′W	ET	9. 8.66
Atlantis II	121	4800	327	35°50.0′N	65°11.0′W	ET	21. 8.66
24	122	4833	108	35°50.0′N	64°57.5′W	ET	21. 8.66
				−35°53.0′N	−64°58.0′W		
	123	4853	377	37°29.0′N	64°14.0′W	ET	22. 8.66
	124	4862	179	37°26.0′N	63°59.5′W	ET	22. 8.66
				−37°25.0′N	−63°58.0′W		
	125	4825	498	37°24.0′N	65°54.0′W	ET	23. 8.66
				−37°26.0′N	−65°50.0′W		
	126	3806	56	39°37.0′N	66°47.0′W	ET	24. 8.66
				−39°37.5′N	−66°44.0′W		
Atlantis II	175	4667–4690	387	36°36.0′N	68°29.0′W	ES	29.11.67
40				−36°36.0′N	−68°31.0′W		
GUINEA BASIN							
Walda	DS20	2514	1	02°32.0′S	08°18.1′E	DS	
	DS31	4279	43	03°17.5′N	02°01.7′E	DS	
CAPE VERDE BASIN							
Atlantis II	147	2934	29	10°38.0′N	17°52.0′W	ES	6. 2.67
31	148	3814–3828	197	10°37.0′N	18°37.0′W	ES	7. 2.67
	149	3861	579	10°30.0′N	18°18.0′W	ES	7. 2.67
BRAZIL BASIN							
Atlantis II	156	3459	1	00°46.0′S	29°28.0′W	ES	14. 2.67
31				−00°46.5′S	−29°24.0′W		
ARGENTINE BASIN							
Atlantis II	242	4382–4402	3	38°16.9′S	51°56.1′W	ES	13. 3.71
60	256	3906–3917	75	37°40.9′S	52°19.3′W	ES	24. 3.71
	259	3305–3317	4	37°13.3′S	52°45.0′W	ES	26. 3.71
WEST EUROPE BASIN							
Chain 106	326	3859	7	50°04.9′S	14°23.9′W	ES	22. 8.72
				−50°05.3′S	−24°24.8′W		
	328	4400	45	50°04.7′S	15°44.8′W	ES	23. 8.72
	330	4632	12	50°43.5′S	17°51.7′W	ES	24. 8.72
				−50°43.4′S	−17°52.9′W		
	335	3882–3919	22	40°25.3′S	46°30.0′W	ES	31. 8.72
Jean Charcot	DS23	4734	5	46°32.8′N	10°21.0′W	ES	26.10.72
(Polygas)	DS20	4226	1	47°33.0′N	09°36.7′W	ES	24.10.72
(Biogas II)	DS30	4106	1	47°38.3′N	09°33.9′W	DS	18. 4.73
(Biogas III)	DS45	4260	1	47°33.9′N	09°38.4′W	DS	27. 8.73
	DS46	4521	6	46°28.6′N	10°23.0′W	DS	29. 8.73
(Biogas IV)	DS53	4425	35	44°30.4′N	04°56.3′W	DS	19. 2.74
	DS54	4659	19	46°31.1′N	10°29.1′W	DS	21. 2.74
	DS55	4125	16	47°34.9′N	09°40.9′W	DS	22. 2.74
	DS56	4050	3	47°32.7′N	09°28.2′W	DS	23. 2.74
(Biogas V)	DS66	3480	1	47°28.2′N	09°00.0′W	DS	16. 6.74
	DS68	4550	2	46°26.7′N	10°23.9′W	DS	19. 6.74
	DS69	4510	6	44°21.9′N	04°52.4′W	DS	20. 6.74
(Biogas VI)	DS75	3250	4	47°28.1′N	09°07.8′W	DS	22.10.74
	DS76	4228	30	47°34.8′N	09°33.3′W	DS	23.10.74
	DS77	4240	6	47°31.8′N	09°34.6′W	DS	24.10.74
	DS78	4706	29	46°31.2′N	10°23.8′W	DS	25.10.74
	DS79	4715	21	46°30.4′N	10°27.1′W	DS	26.10.74
	DS80	4720	6	46°29.5′N	10°29.5′W	DS	27.10.74
	DS81	4715	4	46°28.3′N	10°24.6′W	DS	27.10.74
	DS84	4466	82	44°30.0′N	04°53.9′W	DS	29.10.74
	DS85	4462	16	44°23.2′N	04°50.8′W	DS	30.10.74
	CP13	4134	1	47°34.4′N	09°38.0′W	CP	23.10.74
	CP14	4237	4	47°32.0′N	09°35.9′W	CP	23.10.74
	CP16	4825	3	46°27.3′N	10°25.8′W	CP	25.10.74
	CP17	4706	2	46°30.8′N	10°19.5′W	CP	26.10.74
	CP20	4459	1	44°23.2′N	04°51.4′W	CP	29.10.74
	CP21	4453	1	44°21.2′N	04°49.3′W	CP	30.10.74
	CP22	4475	6	44°22.9′N	04°54.8′W	CP	30.10.74
Jean Charcot	CP10	4823	11	48°25.5′N	15°10.7′W	DS	31. 7.76
(Incal)				−48°26.3′N	−15°09.8′W		
	DS11	4823	5	48°18.8′N	15°11.5′W	DS	1. 8.76
				−48°13.6′N	−15°12.0′W		
	WS03	4829	41	48°19.2′N	15°23.3′W	WS	1. 8.76
				−48°19.1′N	15°22.5′W		
	CP11	4823	5	48°20.4′N	15°14.6′W	CP	1. 8.76
				−48°21.2′N	−15°13.7′W		
	0S02	4829	14	48°19.2′N	15°15.9′W	OS	2. 8.76
				−48°19.1′N	−15°15.5′W		
	WS04	4829	1	48°18.9′N	15°15.9′W	WS	2. 8.76
				−48°19.1′N	−15°15.5′W		
	WS07	4281	21	47°30.6′N	09°37.1′W	WS	7. 8.76
				−47°31.2′N	−09°35.7′W		
	0S05	4296	5	47°31.3′N	09°34.6′W	OS	
				−47°32.2′N	−09°34.7′W		
	DS14	4254	8	47°32.6′N	09°35.7′W	DS	7. 8.76
				−47°32.9′N	−09°35.1′W		
	DS15	4211	3	47°33.4′N	09°39.1′W	DS	8. 8.76
				−47°33.8′N	−09°38.5′W		
	WS0S	4287	61	47°30.5′N	09°33.7′W	WS	9. 8.76
				−47°29.3′N	−09°34.1′W		
	0S06	4316	27	46°27.3′N	09°36.2′W	OS	9. 8.76
				−47°27.9′N	−09°36.0′W		
	DS16	4268	14	47°29.8′N	09°33.4′W	DS	9. 8.76
				−47°30.3′N	−09°33.4′W		
	0S07	4249	22	47°31.8′N	09°34.3′W	OS	10. 8.76
				−47°31.3′N	−09°34.3′W		
	KR17	4268	1	47°31.2′N	09°32.0′W	KR	10. 8.76
				−47°31.3′N	−09°34.3′W		
	WS09	4277	61	47°28.8′N	09°34.0′W	WS	10. 8.76
				−47°27.9′N	−09°34.0′W		
	WS10	4354	149	47°27.3′N	09°39.9′W	WS	11. 8.76
				−47°28.2′N	−09°39.9′W		
	0S08	4327	12	47°29.8′N	09°39.2′W	OS	11. 8.76
				−47°29.5′N	−09°38.8′W		
VEMA FRACTURE							
Jean Charcot	DS01	5097	1	10°57.2′N	45°07.6′W	DS	14.11.77
(Biovema)				−10°57.2′N	−45°07.1′W		
	DS03	5150	21	10°47.1′N	42°40.74′W	DS	16.11.77
				−10°47.19′N	−42°40.35′W		
	DS04	5100	18	10°46.38′N	42°41.38′W	DS	17.11.77
				−10°46.76′N	−42°41.11′W		
	KR05	5100	2	10°47.45′N	42°40.34′W	KR	17.11.77
	DS05	5100	32	10°45.97′N	42°40.29′W	DS	18.11.77
				−10°46.08′N	−42°39.85′W		
	CP05	5100	2	10°46.23′N	42°40.41′W	CP	19.11.77
				−10°46.36′N	−42°39.75′W		
	KG12	5100	1	10°47.5′N	42°40.41′W	KG	20.11.77
	DS09	5875	57+ 1V	11°36.4′N	32°51.8′W	DS	25.11.77
				−11°37.1′N	−32°51.3′W		

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
	DS10	5875	1	11°36.8′N −11°36.9′N	32°52.5′W −32°52.8′W	DS	25.11.77
	DS11	5867	89	11°37.5′N −11°37.6′N	32°53.8′W −32°52.8′W	DS	26.11.77
				CAPE BASIN			
Jean Charcot (Walvis)	DS01	5205–5240	2	33°53.9′N −33°53.9′S	05°05.9′W −05°06.4′W	DS	24.12.78
	DS02	5280	23	33°54.7′S	05°07.3′E −05°07.7′E	DS	25.12.78
	DS03	4657	1	33°21.8′S	02°40.4′E	DS	28.12.78
	KG05	5235	1	33°54.5′S	05°08.5′E	KG	25.12.78
	KG06	5210	1	33°54.2′S	05°09.2′E	KG	26.12.78
	KG08	5211	1	33°54.7′S	05°09.0′E	KG	26.12.78
	KG13	4560	1	33°22.7′S	02°36.8′E	KG	29.12.78
	DS05	4560	34	33°20.5′S	02°34.9′E	DS	30.12.78
	CP01	5040	3	33°53.6′S	05°06.7′E	CP	24.12.78
	CP05	4500	1	33°22.9′S −33°26.2′S	02°36.0′E −02°34.6′E	CP	30.12.78
	DS06	4585	22	33°24.5′S	02°32.9′E	DS	31.12.78
				ANGOLA BASIN			
(Walvis)	DS07	5100–5214	18	26°59.7′S −27°00.2′S	01°07.1′E −01°05.8′E	DS	3. 1.79
	DS08	5225	1	29°59.6′S	01°07.3′E	DS	5. 1.79
	DS09	5220	4	26°59.9′S −27°00.0′S	01°06.7′E −01°06.2′E	DS	6. 1.79

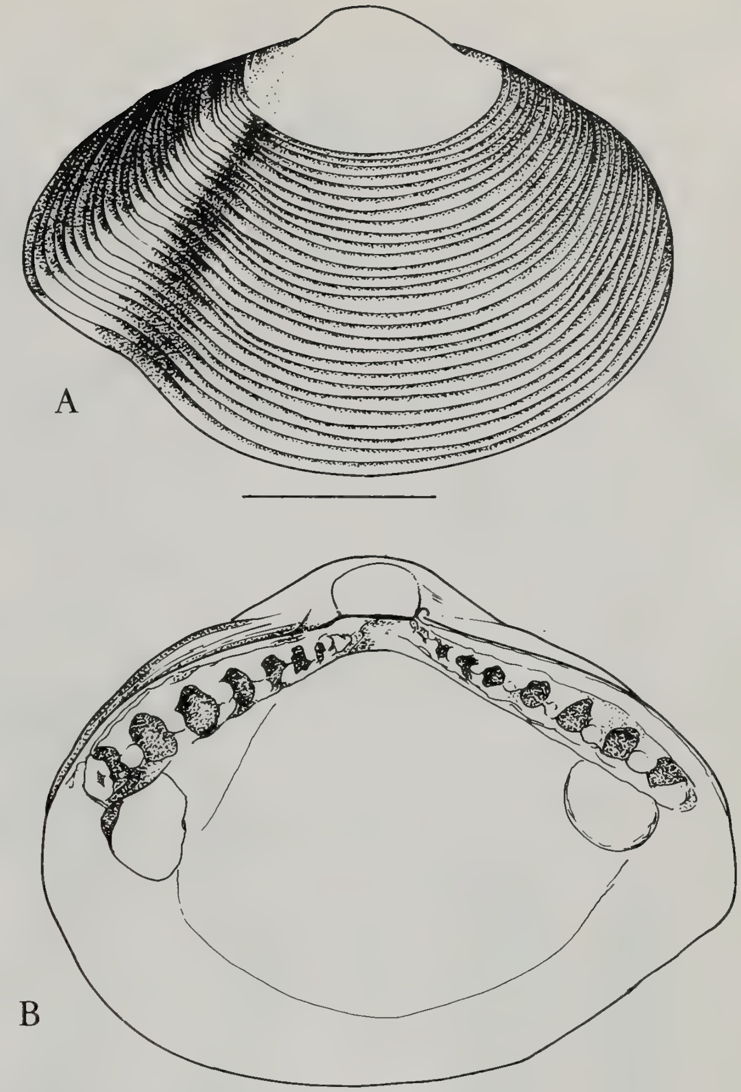

Fig. 63 *Ledella ultima*: (a) Right lateral external view of the Holotype specimen (BMNH No. 1887.2.9.3354) (note margin not thickened); (b) internal view of right valve of specimen with thickened margin from Station 175. (Scale = 1 mm).

Although there are recent descriptions of the shell of *L. ultima* (Knudsen, 1970; Warén 1978) with the advantage of large numbers of samples and many thousands of specimens we have been able to assemble much more information on population variations.

DEPTH RANGE. 1330–5875 m

DESCRIPTION (Figs. 63–65). Shell solid, inflated, equilateral or almost so (postumbonal length 40–56% of total length depending on size), ornamented with sharp concentric ridges, slightly broader ventrally becoming narrow and fainter towards umbo with smooth area around umbo of varying width; umbos prominent, medially directed; dorsal margin convex, antero-dorsal margin forms smooth broad sloping curve with anterior margin, proximal postero-dorsal margin almost straight between umbo and distal end of hinge plate, distal margin short, deeply convex, forming relatively blunt rostrum which with posterior ventral sinuous margin gives 'hooked' appearance, ventral margin smooth curve, ill-defined rounded ridge from umbo to rostrum, in large specimens ventral margin may be thickened to form a flattened edge; hinge plate broad, solid, anterior and posterior plates each with up to 6–10 chevron teeth (number varying with size); internal ligament amphidetic rectangular in outline; adductor and pallial scars usually visible.

Larval shell length: 310 μm, maximum recorded shell length: 3.40 mm.

MORPHOLOGY. *Ledella ultima* differs from all other *Ledella* species described here in having the hind gut spirally coiled on the right side of the body (Figs. 66 & 67). The only other described *Ledella* species with this type of gut configuration is *L. kermadecensis* (Knudsen, 1970).

Other morphological features are similar to those described for the other species (Fig. 66). The mantle edge is relatively well developed, the inner fold being moderately broad. The combined siphon is not fused ventrally and is fairly small. A very fine siphonal tentacle, often difficult to observe, is attached close to the base of the siphonal embayment on the right or the left side. The anterior sense organ is more ventrally situated than in other species. The adductor muscles are large, approximately equal in size and round in shape. The gills lie parallel to the posterior dorsal margin with 8–11 gill plates. The labial palps are large with 14–20 ridges and with long, thin palp proboscides. The foot is large, deeply cleft with a very large 'byssal' gland (Fig. 68).

The stomach and style sac lie ventral to the umbos, they are relatively small, extending only into the upper third of the foot, posterior to the pedal ganglion. From the style sac the hind gut passes posterior and ventral to the pedal ganglion before retracing its path to the dorsal margin and then to the right side of the body where it forms a series of coils. These usually number 12 although exceptionally 13 have been observed. One individual was also observed with an additional loop to the left side of the body. The coils are stacked in an overlapping sequence dorsally and antero-laterally to the viscera. Some coils lie internal to the others, thus, a variable number of coils is immediately visible in lateral view, the most common number being eight. The extent of the area covered by the coils also varies, depending on the compactness and shape of the coils, which may be circular or oval in outline.

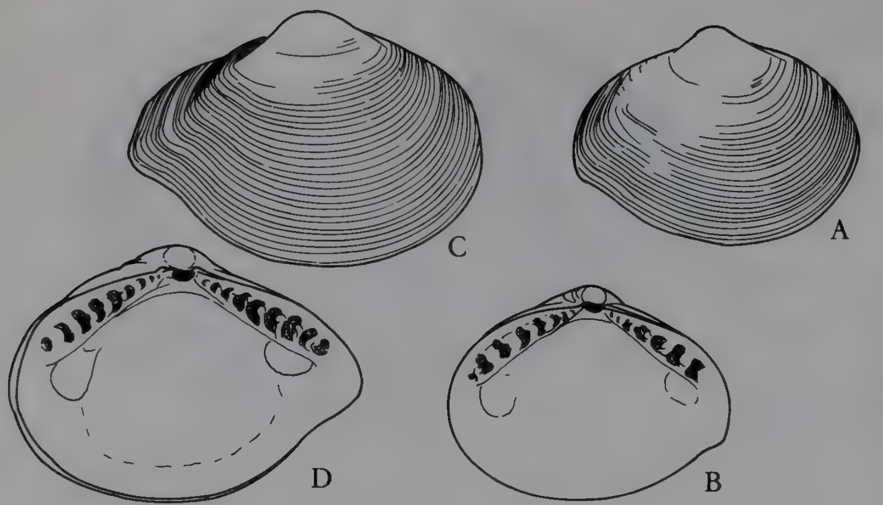

Fig. 64 *Ledella ultima*: (a) & (b) Right lateral external view and internal view of right valve of the type specimen of *L. bushae* (note margin not thickened), (c) & (d) Right lateral external view and internal view of right valve of type of *L. crassa* (note margin thickened). See p. 161 & Fig. 73 for details of variation in shape. (Scale = 1 mm).

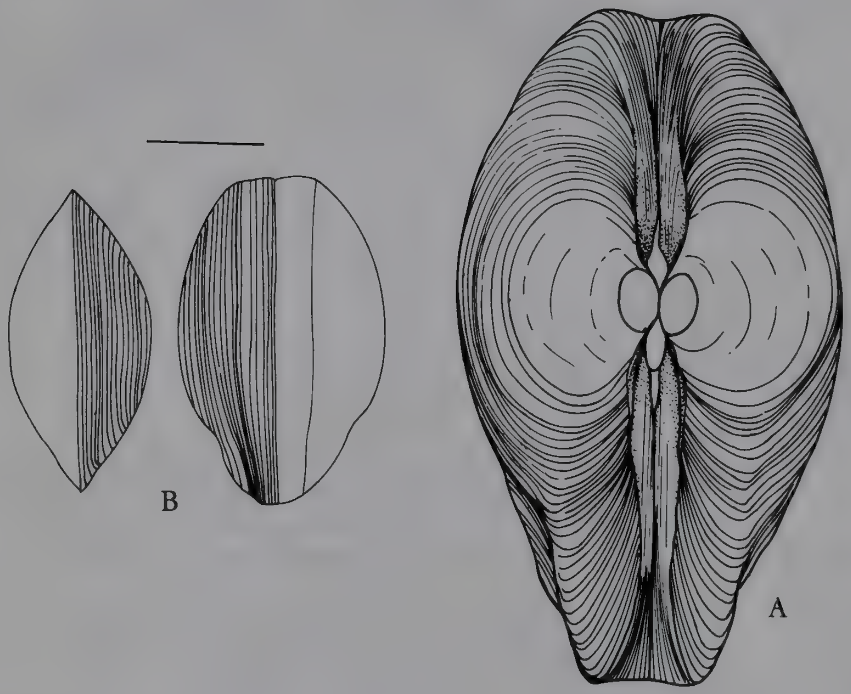

Fig. 65 *Ledella ultima*: (a) Dorsal view of shell with thickened margin from Station Biogas V DS69; (b) Ventral view of specimens of similar size, one with and the other without a thickened margin, from the North America Basin.

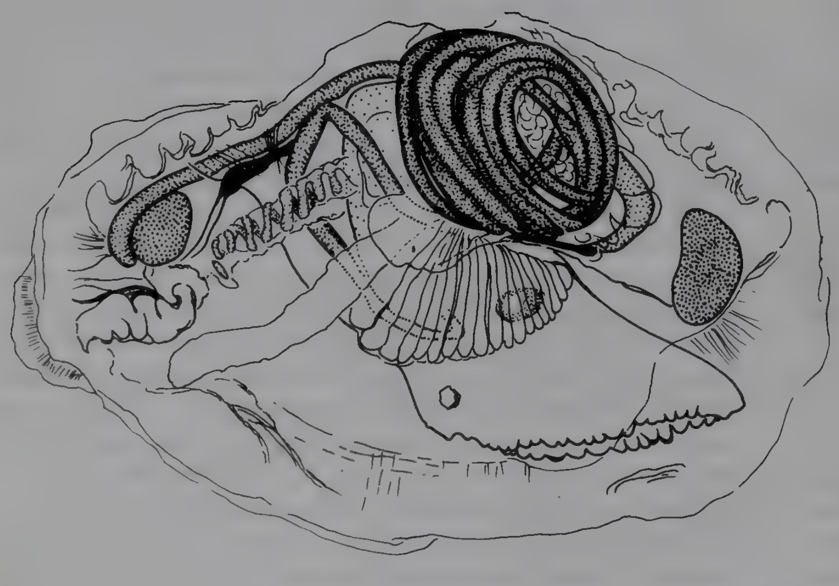

Fig. 66 *Ledella ultima*: Lateral view of specimen from the right side with shell removed to show the arrangement of body organs. For identification of parts see Fig. 42. (Scale = 1 mm).

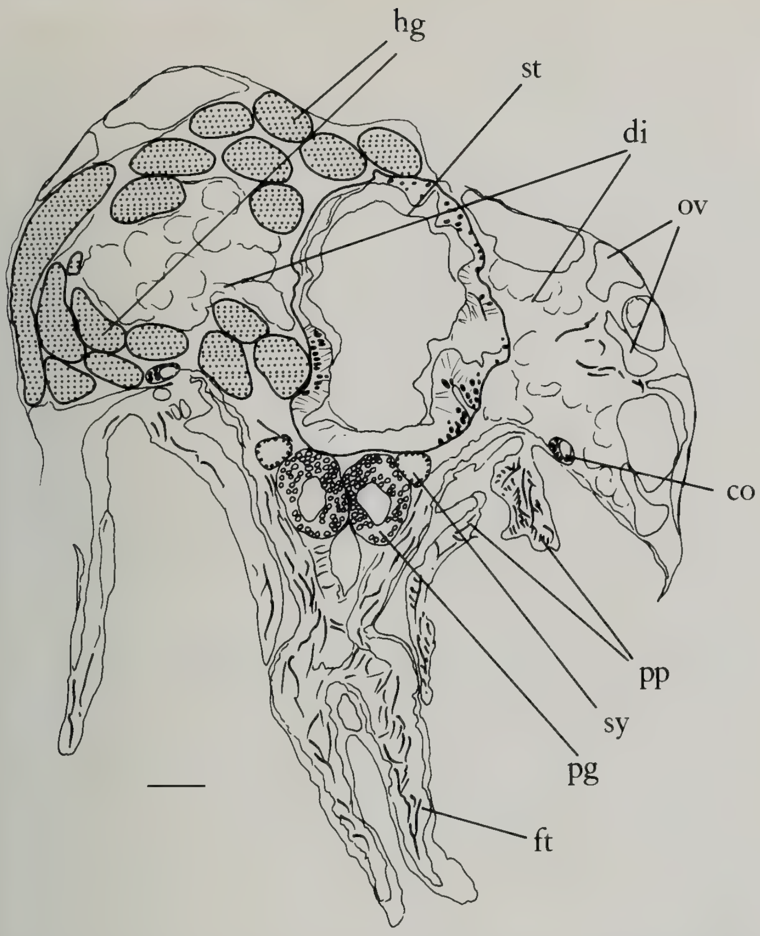

Fig. 67 *Ledella ultima*: Vertical transverse section through stomach and hind gut coil as viewed from anterior side (i.e. morphological right is topographically left). (Scale = 0.1 mm).

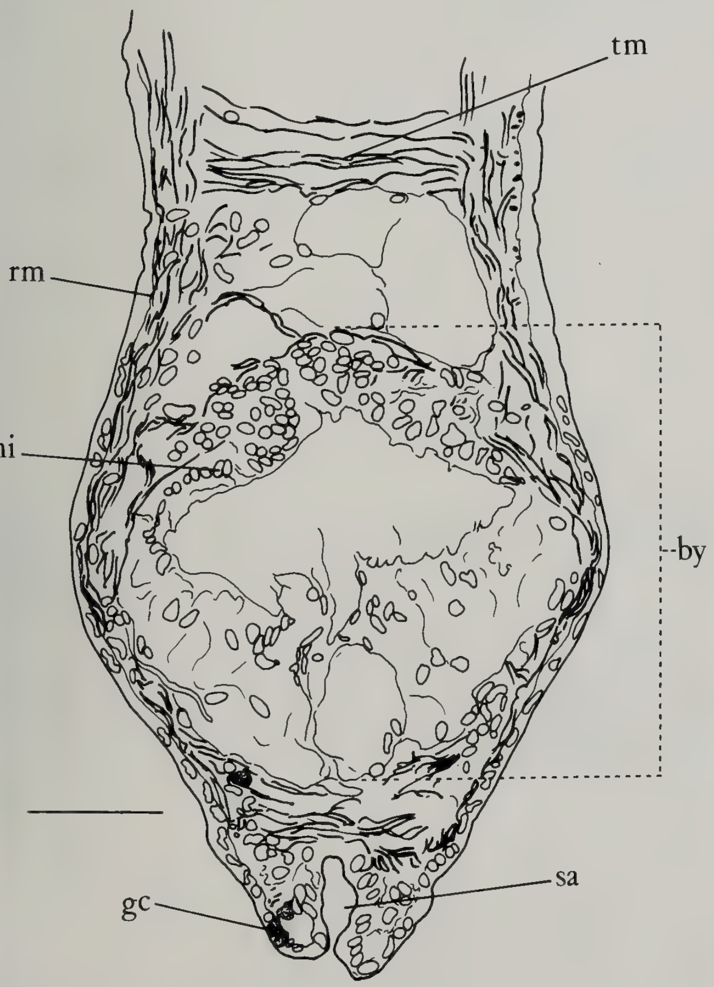

Fig. 68 *Ledella ultima*: Vertical transverse section through heel of the foot and the 'byssal' gland. (Scale = 0.1 mm).

The pedal ganglia are large (Fig. 67). The cerebral and visceral ganglia are smaller and club-shaped, the visceral ganglia lying anterior to the posterior adductor muscle.

The smallest individual recorded with discernible gonads was 2.4 mm in length. Development was assessed in two samples, one from the western Atlantic (Sta. 101) and the other from the eastern Atlantic (BGIV DS53). The maximum diameter of the ova in different mature individuals varied from 160–280 µm (Sta. 101) and from 220–255 µm (BGIV DS53). Ova were few in number, 6–29 per individual at both Stations most being in the left side of the body, diametrically opposite to the coils of the hind gut. Individuals from Station 101 with thickened shell margins (› 0.6 mm) were compared with ones without a thickened margin (‹ 0.1 mm) but of comparable total shell length. Overall fewer ova which tended to be smaller were present in those with no thickening of the margin (Table 1).

The percentage of the lateral body covered by testis ranged from 0.5% (2.5 mm total length) to 19% (2.9 mm total length) in individual specimens examined from Station BGIV DS53 and 4.5% (2.87 mm total length) to 16.5% (2.5 mm total length) at Station 101.

Table 1. Comparison of numbers of ova in specimens with and without thickened shell margins

Not Thickened			Thickened			
Shell length	Max Diam. of ova	Number of ova	Shell length	Max Diam. of ova	Number of ova	Thickness of ventral margin (mm)
2.79	160µm	6	2.79	210µm	20	0.82
2.81	220µm	9	2.81	210µm	29	0.90
2.83	160µm	8	2.81	240µm	14	1.64
2.89	240µm	10	2.83	260µm	11	0.90
			2.97	280µm	25	0.66*

* partially spent.

During the course of growth, there is little change in the relative position of the umbo. In very small individuals it is usually posterior to the midline but with increasing length, it becomes more central in position. Although there is a slight increase in height/length ratio with increasing length, considerable variation was observed. It should be noted that analysis of the width/length ratio is complicated by the thickening of the shell margin (Fig. 69).

Thickening of the shell margin to form a flattened edge may be present in individuals › 2.4 mm in length, however, not all individuals above this length exhibit thickening (Fig. 70). The maximum recorded thickening was 1.3 mm in an individual shell 2.5 mm in length. The feature is formed following a sharp change in the spiral angle of growth of the shell to produce a flattened edge. While not a unique occurrence among deep sea protobranchs it is by far seen at its most extreme in *Ledella ultima*. It is possible that it may be a feature of those specimens that are maturing for a second or more time.

Because of the multiplicity of names given to this species, various shell parameters from samples from different basins of the Atlantic were measured and compared (Figs. 69, 71, 72 & 73). The Stations selected were:- Walda DS31 (Guinea

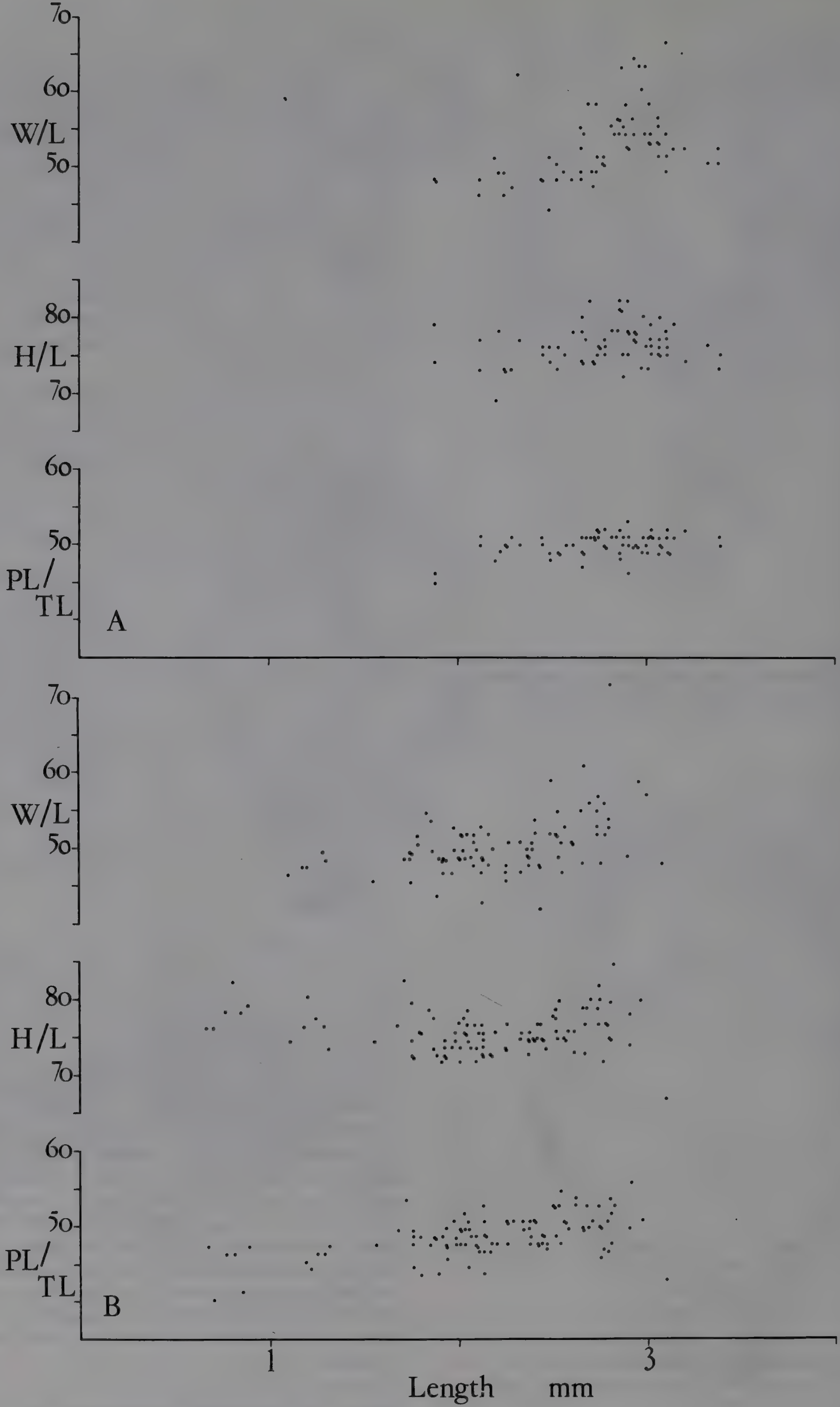

Fig. 69 *Ledella ultima*: (a) & (b) Analysis of change in shape with growth as shown by the ratios posterior umbo length/total length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 122 and Station Biogas VI DS84. Fig. 70.

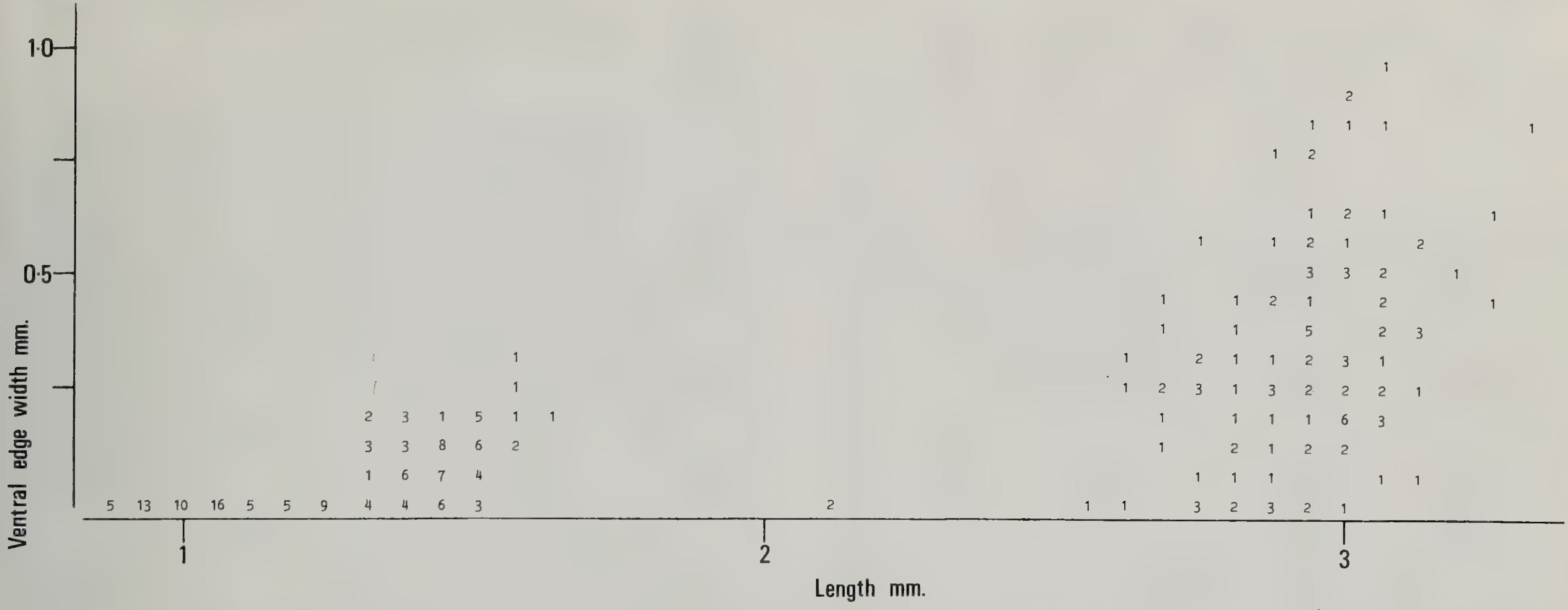

Fig. 70 *Ledella ultima*: An analysis of the width of the ventral shell margin plotted against length of specimens taken at Station 78.

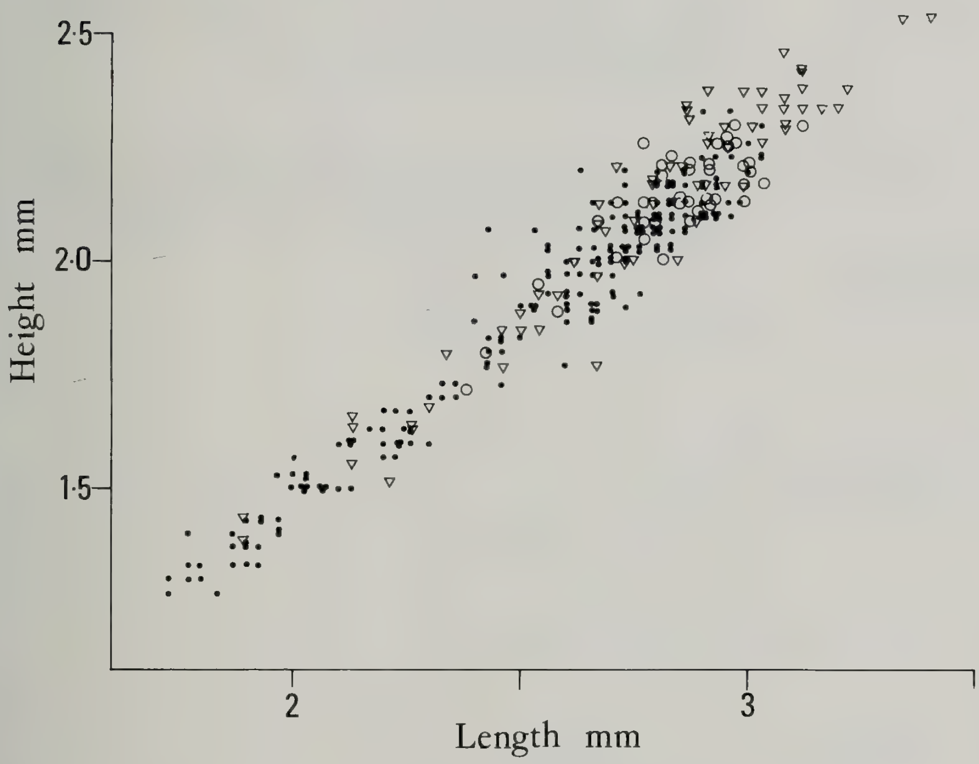

Fig. 71 *Ledella ultima*: The relationship between shell height and length compared for three Stations 148 (points) Walda DS31 (open circles) and Biogas VI DS84 (open triangles).

Basin), Sta. 148 (Cape Verde Basin), BGVI DS84 (W. European Basin), Sta. 101 (N. American Basin), Sta. 122 (N. American Basin) (Table 3).

Also, because of the very large numbers in the collections of this cosmopolitan species occurring over a wide band of abyssal depths it was possible to carry out a detailed statistical appraisal of the length, height and width relationships between and within populations. In short such differences as were found between populations were not statistically significant.

In this overall comparison the only difference between western and eastern Atlantic populations, and this is a visual one, is that North American specimens tend to have a less pointed rostrum with a more shallow ventral margin sinuosity, are slightly more rounded in outline, and the position of the umbo is slightly more variable but slightly more posterior on average. However, the variation within any sample is large (Fig. 74). No differences in internal morphology were observed.

Examination of the type specimens of *L. ultima, L. bushae* and *L. crassa* show some difference in the shape and thickness of the ornamental concentric ridges, but these differences are within the range of variation observed in any large sample of this species from any locality (Figs. 64, 73 & 74).

Despite the fact that a very small number of large eggs is produced by each individual, there seems to have been no evolution of population differences in the different abyssal basins let alone evolution of sibling species. Thus, the genus *Ledella* and *L. ultima* in particular, is in sharp contrast to the genus *Malletia* where varieties and sibling species are common (Sanders & Allen, 1982). This may be but a consequence of the commonness and continuum in the deep sea of *L. ultima*. There are clearly other possible explanations, the most likely being that in common with most other protobranchs, there has been little genetic change over many geological eras and over the entire geographic range of the species.

One of the notable aspects of size frequency histograms (Fig. 75) in all populations is the marked right hand skewness seen in all. In each case the maximum length observed is about 3.0 mm. This type of skewed histogram is typical of deep sea bivalves in which there are no large individual settlements of larvae. In shallow water species settlement followed by massive mortality results in histograms skewed to the left. In the case of *L. ultima* the right hand skew is compounded by the change in direction of shell growth. What initiates this change in growth is not clear, but it is tempting to postulate that this occurs after the release of the first batch of gametes. The advantage of small size to an abyssal benthic animal have been pointed out elsewhere (Allen 1978) yet it may be that this change gives advantage in that for no increase in lateral area of shell the volume of the mantle space is significantly increased. This allows for a marked increase in the number of eggs that can be accommodated and hence the breeding success of the species. It is also tempting to speculate that the greatly increased length of the hind gut accommodated by the tight coils, allows for increased assimilation of digested food and energy supply, which will also have reproductive advantage in this species.

DISTRIBUTION. This is by far the most common and cosmopolitan protobranch species and is truely abyssal. N. American, Canary, Argentine, Angola and Agulhas Basins, Guinea Basin and Scotia Sea.

DEPTH RANGE. 3196–5130 m.

Table 2. Relationship between geographical distribution, depth of occurrence and hindgut morphology in species of *Ledella*

Species	Depth range (m)	Distribution	Rarity	Hind gut
L. p. hampsoni	2051–2357	Cape Verde	C	sl l & r
L. p. pustulosa	609–2659	S European–Canaries	C	sl l & r
L. p. marshalli	2496–4796	NW Scotland–SW Ireland	C	sl l & r
S. p. argentinae	3305–5223	Argentine	C	sl l & r
L. modesta	1661–4632	E European–Sierra Leone NE USA – Argentine	C	sl l & r
L. jamesi	1456–2853	Argentine – Guiana	C	sl l & r
L. lusitanensis	1624–1995	Biscay-Cape Verde	R	sl l & r
L. sandersi	1546–2154	SW Africa	MC/R	sl r
L. similis	1336	Biscay	R	sl r
S. verdiensis	3150–3155	Cape Verde	R	sl r
L. oxira	678–1493	SE USA-Argentine	R	sl r/l
L. galatheae	4279–4829	European-SW Africa	R	sl r/c
L. solidula	1000–1830	Surinam-Bermuda	MC	sl r/c
L. acuminata	475–1427	Bay of Biscay	MC	sl r/c
L. ultima	3196–5130	Cosmopolitan	C	c r
L. parva	450–960	E. USA	R	tl r & sl l

C = common; MC = moderately common; R = rare.
c = coil; l = left; r = right; r/c = loop on right passing to left close to anterior adductor then coiling; r/l = loop on right passing to left close to anterior adductor; sl = single loops; tl = two loops.

Table 3. Comparison of shell dimensions in populations of *Ledella ultima*

Station	Max. Length mm	Max. VSM* mm	H/L Average**	H/L Range	W/L Average**	W/L Range	P.UL/TL Average**	P.UL/TL Range
WALDA DS31 (Guinea Basin) N=42	3.12	0.62	0.75±0.021	0.71−0.79	0.56±0.035	0.47−0.62	0.51±0.013	0.47−0.52
Stn. 122 (N. American B) N=106	3.10	0.82	0.76±0.026	0.71−0.84	0.50±0.035	0.41−0.60	0.48±0.030	0.40−0.55
Stn. 101 (N. American B) N=330	3.04	1.31	0.76±0.026	0.68−0.84	0.57±0.063	0.45−0.82	0.48±0.044	0.42−0.56
Stn. 148 (Cape Verde Basin) N=208	3.06	0.90	0.74±0.032	0.69−0.85	0.53±0.059	0.41−0.69	0.51±0.016	0.47−0.53
BGVI DS84 (W. European Basin) N=68	3.40	1.11	0.76±0.037	0.69−0.82	0.53±0.048	0.44−0.68	0.50±0.014	0.48−0.53

Note the slight difference between posterior umbonal length/total length between N. American samples and the rest. Umbos slightly more posterior in these than the others but they also have the greatest range.
** ± standard deviation.
* VSM − Maximum width of ventral shell margin.

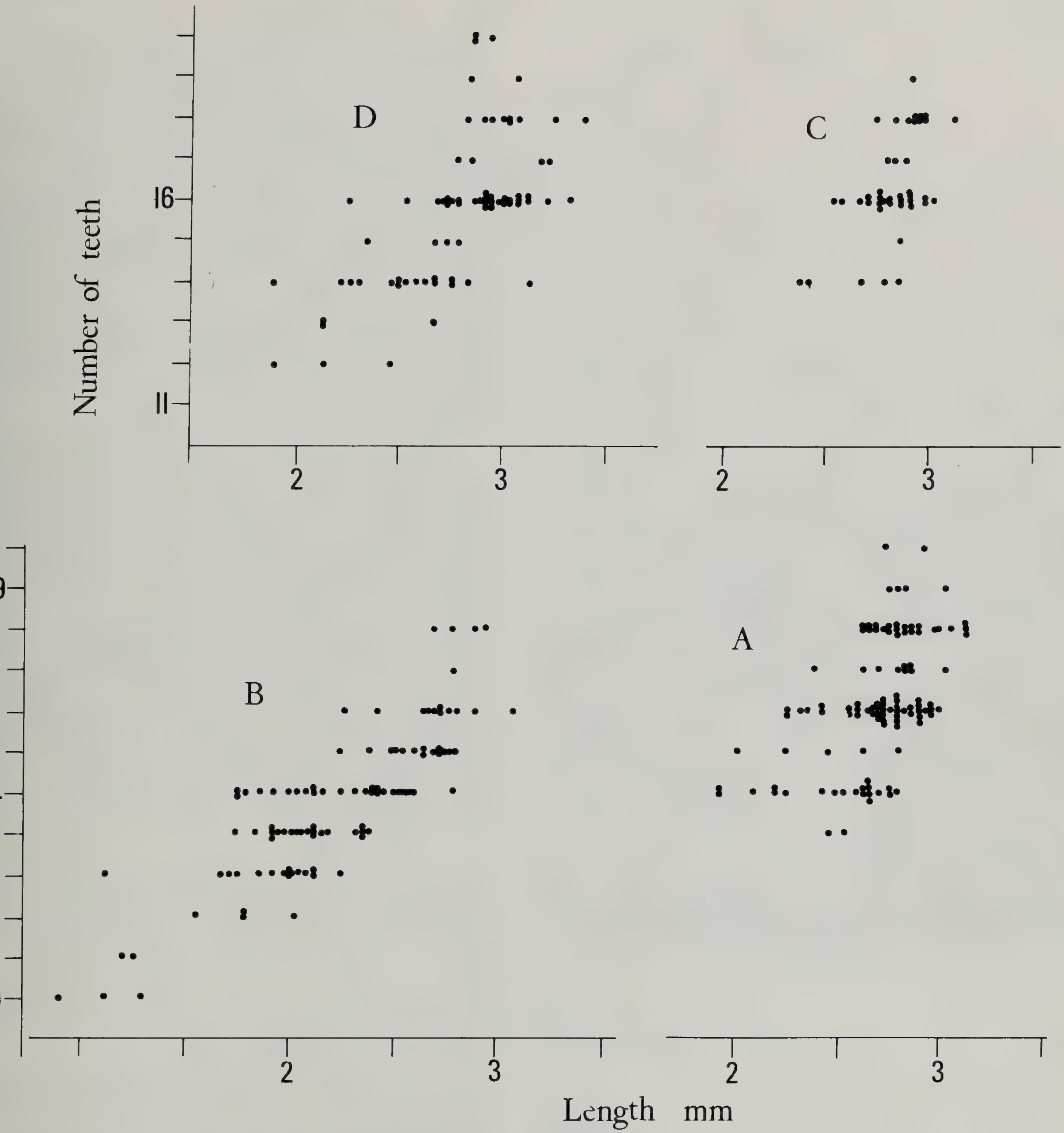

Fig. 72 *Ledella ultima*: The relationship between numbers of hinge teeth and shell length for four Stations a) 148; b) 122; c) Walda DS31 and d) Biogas VI DS84.

Ledella parva Verrill & Bush 1897

HOLOTYPE. U.S. National Museum (USNM) No. 78365.

TYPE LOCALITY. U.S. Fish Comm. Sta. 2689, off Martha's Vineyard, United States, 960 metres.

SYNONYMY. ?*Leda semen* Smith, 1885. *Rep. Lam. Chall. 13*, p. 231, pl. 19, Figs. 2 & 2a.
Ledella parva Verrill & Bush, 1897. *Am. J. Sci. 3*, p. 54, Fig. 18.
Ledella parva Verrill & Bush: Verrill & Bush, 1898. *Proc. U.S. natn. Mus. 20*, p. 857, pl. 81, Fig. 1.
Leda aspecta Dall 1927. *Proc. U.S. natn. Mus. 70*, art. 18, p. 9.
Nuculana semen (Smith): James, 1972. Ph.D. Thesis Texas A & M Univ. p. 119, Figs. 75 & 76.

MATERIAL.

Cruise	Sta.	Depth(m)	No.	Lat.	Long.	Gear	Date
USNM 78365	2689	960	?	Off Martha's Vineyard			?
Duke Univ. (Grassle)	349	450	2+ 2V	34°16.6′N	75°48.6′W	VV	7. 1.65
	3417	650	1	34°14.8′N	75°46.7′W	ES	29.11.65

Specimens of *Ledella semen* BM(NH) No. 1887.2.9 2925.
No. 1887.2.9. 2921–4.

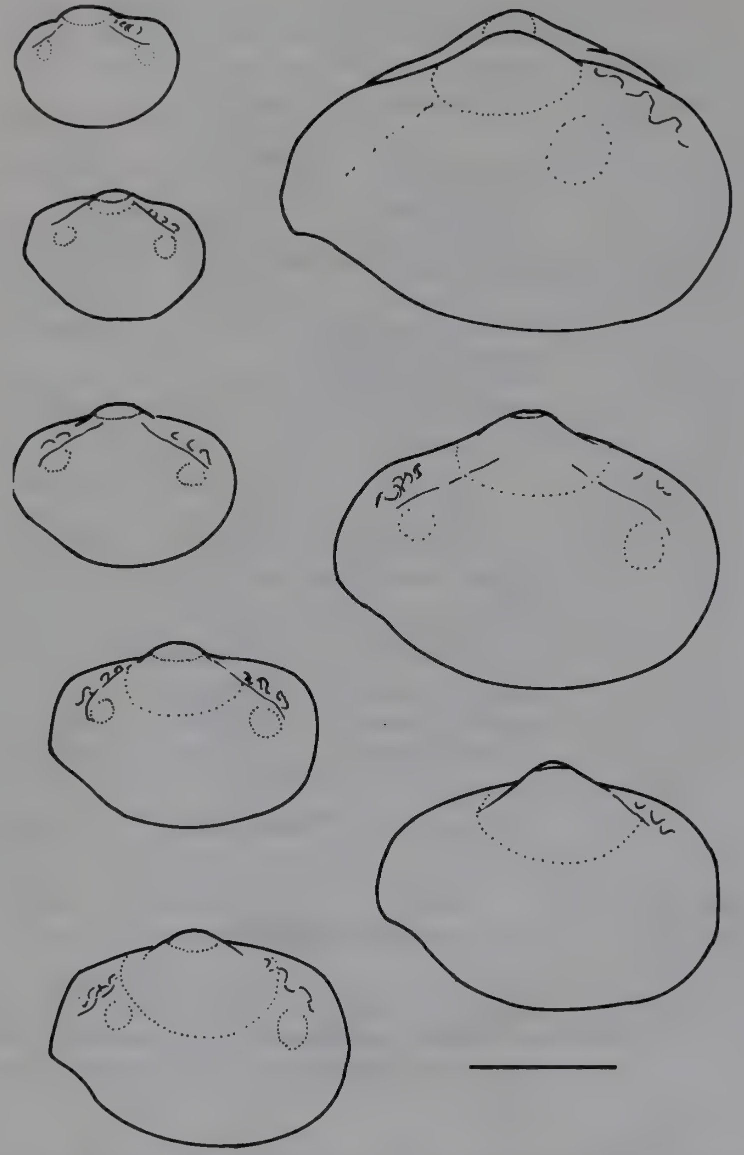

Fig. 73 *Ledella ultima*: Growth series of shells from Station 126 in lateral outline to show change in shape with increasing size. (Scale = 1 mm).

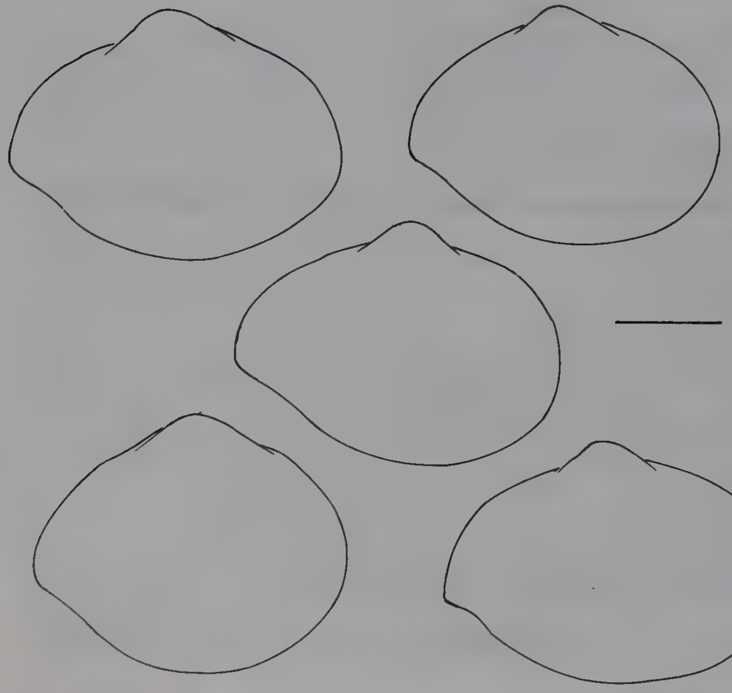

Fig. 74 *Ledella ultima*: Shapes of shells of similar length in lateral outline to show the range of variation within a single sample (Station 84). (Scale = 1 mm).

LOCALITY. Challenger St. 122, off Brazil, 9°05.'S, 34°51'W, 640 m.

Both specimens of *L. semen* labelled 'type' have disintegrated so that it is impossible to make comparisons with the type material of *L. parva* and with the present specimens.

From the descriptions of *L. semen* and *L. parva* and from what little can be made out of the fragments of the type species of *L. semen*, it is possible that *L. parva* and *L. semen* are synonymous. This conclusion was also reached by James (1978). James (1978) noted that Smith (1885) in his original description confused anterior for posterior teeth and *vice versa*. This we confirm. Verrill & Bush (1897) described *L. parva* as a separate species from *L. semen* on the basis of the teeth. Thus, while it may well be that the two species are synonymous, it would be unwise to be categorical. Note too that *L. parva* also resembles *L. oxira* (p. 148) and may be a sibling species.

DESCRIPTION (Figs. 76 & 77). Shell small, ovate, inequilateral, smooth, growth lines very fine; umbos posterior, slightly raised, slightly inclined posteriorly; anterior margin obtusely rounded, posterior margin with short rostrum, antero-dorsal margin curves from umbo in smooth curve with anterior margin, postero-dorsal margin proximally straight, more distally gradually slopes to a point opposite the posterior edge of hinge plate then more steeply to tip of rostrum, posterior ventral margin sinuous, ventral margin rounded, moderately convex, shallow depression in shell from umbo to postero-ventral margin; hinge plate moderately strong, broad, posterior hinge plate short, strongly curved with 9 chevron-shaped teeth, anterior plate less curved with 12 teeth; ligament amphidetic, internal, triangular in shape.

The dimensions of the two intact specimens from Station 349 are as follows:-

Length(mm)	Height(mm)	Width(mm)	H/L	W/L	P.umbo/Total	Teeth Ant/Post
2.6	1.72	valv. sep.	0.66	–	0.40	12/19
1.12	0.84	0.52	0.75	0.46	0.42	–

MORPHOLOGY. Only three specimens were available for study and this description has been based on a single whole mount (Fig. 78).

The mantle structures differ little from those described for the other *Ledella* species. The combined siphon is moderately muscular and elongate, the siphonal tentacle is inserted at the base of the siphon on the left side. The anterior sense organ is anterior to the anterior limit of the anterior adductor muscle. The adductor muscles are large, the posterior muscle is approximately circular in shape while the anterior muscle is larger (1.5x) and bean-shaped in outline.

The foot is large and anteriorly directed. The 'byssal' gland is large. The gills lie deep within the mantle cavity (Fig. 78) but this may be a distortion due to the retracted siphon. Approximately 15 alternating gill filaments are present. The palps are moderately small with 9 ridges and the palp proboscides are elongate and slender. The mouth is situated a short distance behind the anterior adductor muscle and opens into a wide oesophagus to a large stomach. A small style sac penetrates a short distance into the foot. The hind gut penetrates level with the pedal ganglia and then turns 180° passing posterior to the stomach, to the dorsal margin of the

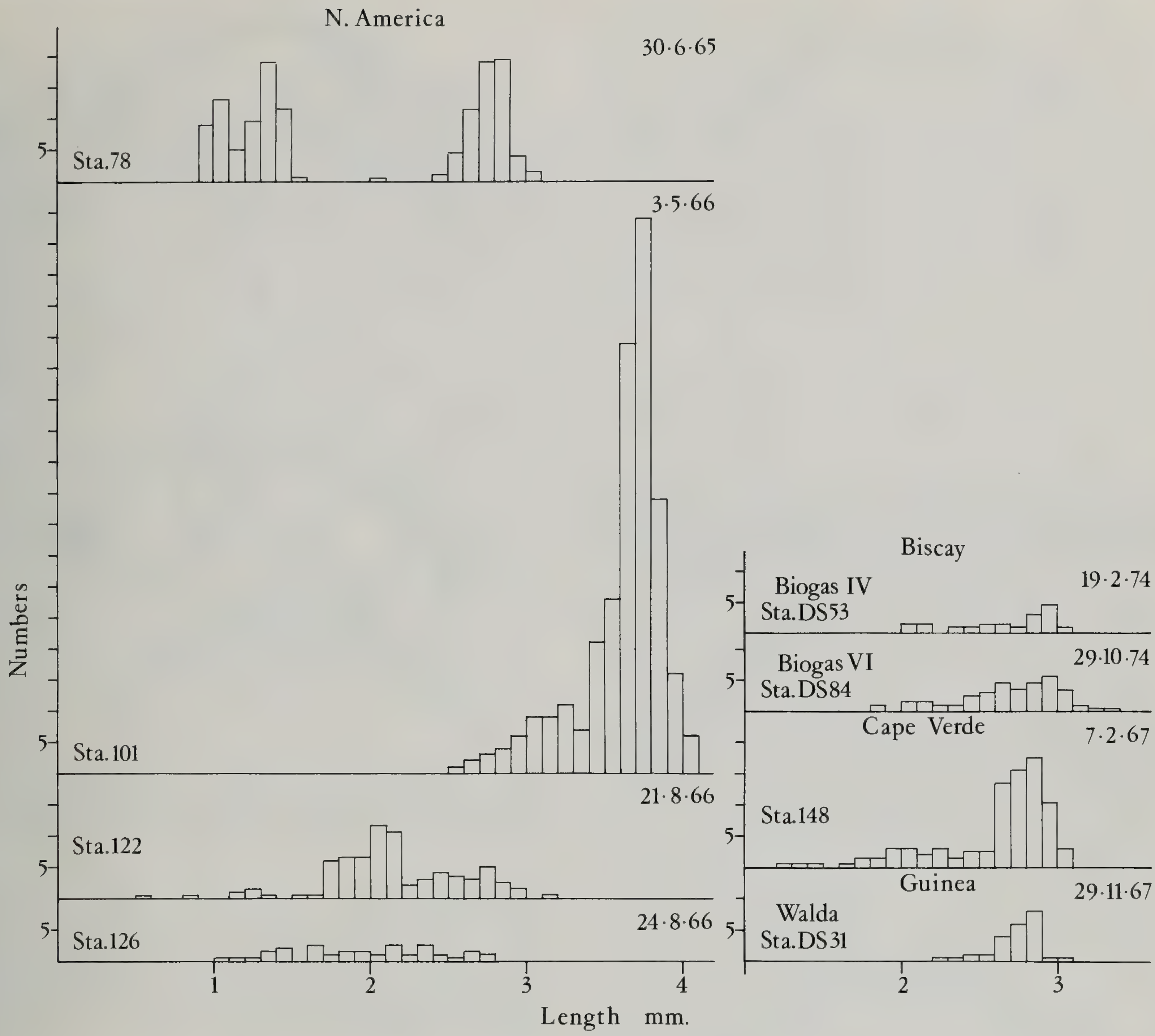

Fig. 75 *Ledella ultima*: Size frequency histograms for samples from eight Stations.

body to form a loop on the right side of the body. Its course takes it close to the anterior adductor muscle and then to a point immediately posterior to the ligament where it crosses to the left side of the body to describe a similar loop to that on the right. Thereafter it passes to the right side for a second time, immediately posterior to the first cross over point, and makes a second loop on the right close to, and in parts superimposed on, the first (Fig. 78). The dorsal section of this second loop passes to the anus posterior to the posterior adductor muscle.

The pedal ganglia are large and situated in the neck of the foot. The visceral and cerebral ganglia are typically cylindrical in shape; the visceral ganglia terminate close to the posterior adductor muscle.

DISTRIBUTION. Upper continental slope off East coast of United States, Gulf of Mexico.

DEPTH RANGE. 450–1180 m.

Ledella sp.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		NORTH ATLANTIC BASIN					
Chain 50	83	5000	1	34°46.5′N	66°30.0′W	ES	3. 7.65
Atlantis II 24	121	4800	1	35°50.0′N	65°11.0′W	ES	21. 8.66
Atlantis II 13	123	3853	1	37°29.0′N	64°14.0′W	ES	22. 8.66

Only three specimens were taken from abyssal depths from the North Atlantic Basin, one of which was an intact dead shell. No whole preparation has been made. As a result we do not wish to define a new species, although we believe that when further specimens are obtained it may well prove to be so. Here we simply record a shell description.

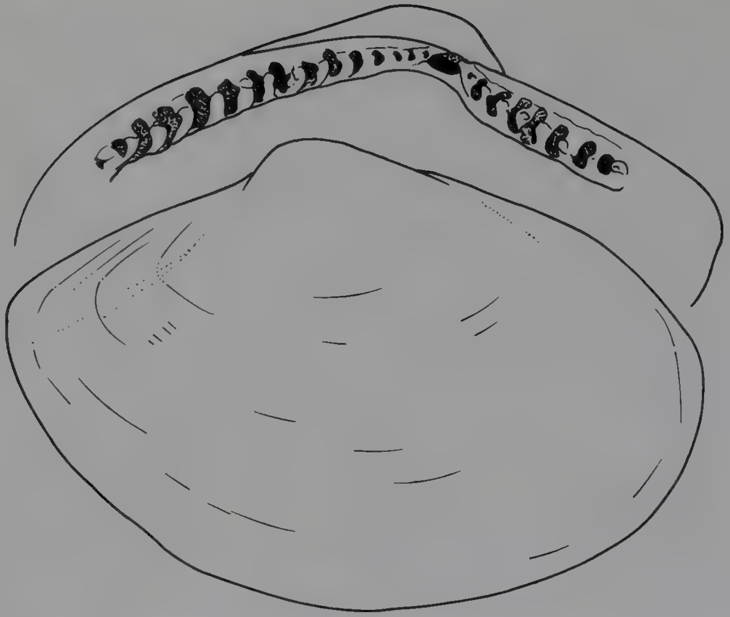

Fig. 76 *Ledella parva*: Right lateral external view of the type specimen (USNM No. 78365); and internal view of hinge region of right valve of the same specimen. (Scale = 1 mm).

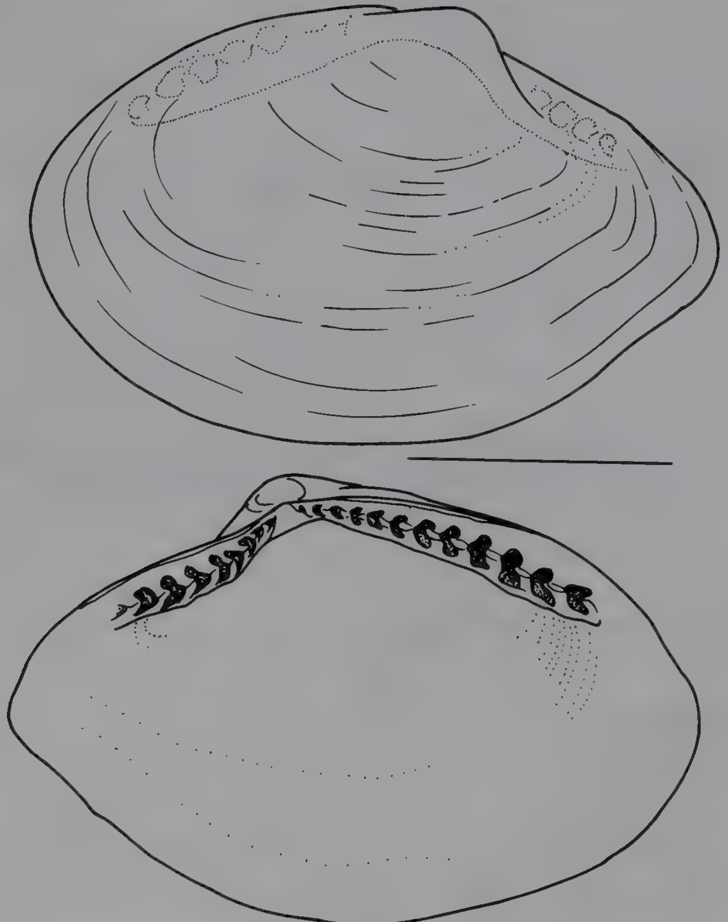

Fig. 77 *Ledella parva*: Left lateral external view of specimen from Duke University Station 349 and internal view of left valve of same specimen to show hinge detail. (Scale = 1 mm).

DESCRIPTION (Fig. 79). Shell robust, ovate, inequilateral, rostrum relatively short, concentric ridges; umbos moderately large, posterior to mid line, directed medially; antero-dorsal margin slopes moderately sharply to curve continuously with narrow anterior margin, postero-dorsal margin slopes moderately sharply to posterior limit of hinge plate to form angle with dorsal margin of rostrum, postero-ventral margin broadly sinuous giving characteristic undercut appearance to shell, rostral ridge moderately strong; hinge plate elongate, fairly broad along entire length, hinge teeth short, broad chevrons except for 3 proximal teeth of anterior and posterior series ventral to umbos; resilifer broad trapezoidal; ligament amphidetic, internal.

Maximum shell length: 5.2 mm.

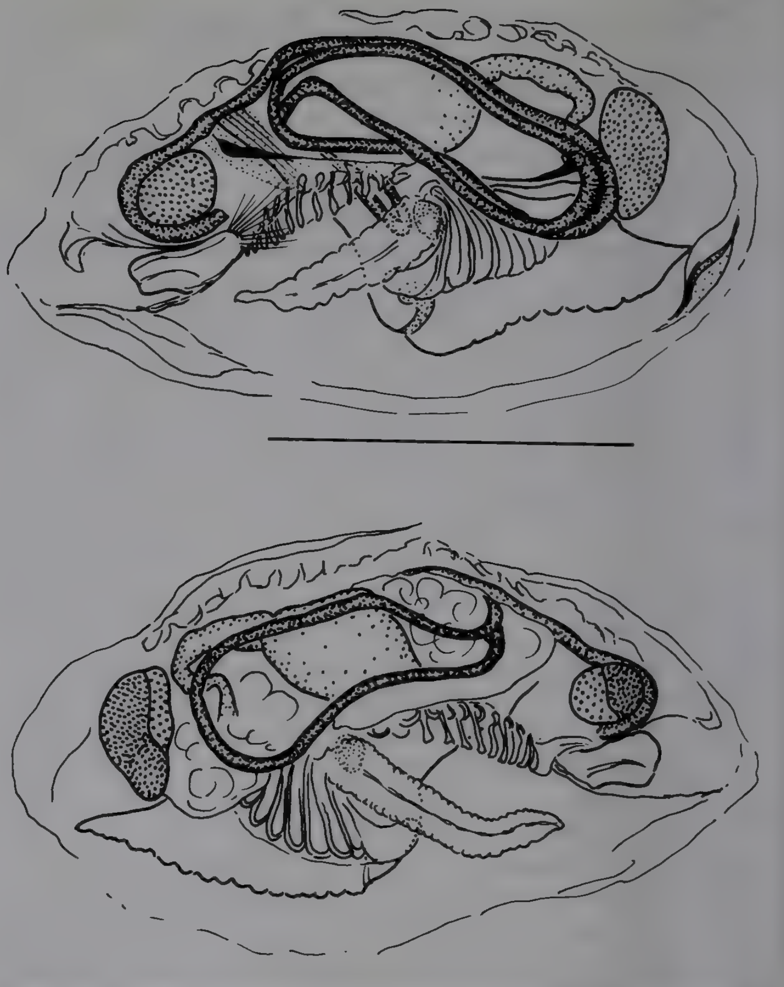

Fig. 78 *Ledella parva*: Lateral view of a specimen from the left and right sides with the shell removed to show the arrangement of the body organs (Station 349). For identification of parts see Fig. 42. (Scale = 1 mm).

DISTRIBUTION PATTERNS

Species of *Ledella* do not occur on the continental shelf. Analysis of the fourteen species described here (Fig. 80, Table 4) shows that most are restricted to the slope and abyssal rise. Many are rare species restricted in their horizontal distribution, for example, *Ledella parva, L. similis* and *L. sandersi* are restricted to the East coast of the USA, Biscay and South West Africa respectively. Others including *L. oxira, L. lusitanensis, L. solidula* and *L. acuminata*, which are a little less rare, spread further along slope, but with either no or relatively little geographical overlap. Rare species also occur at abyssal depths, of these one is the as yet unnamed *Ledella* from the North America Basin, the other *L. verdiensis* is from the Cape Verde Basin.

Of those that remain *L. ultima*, is the most common protobranch in the Atlantic. Except for the Norwegian Basin it occurs throughout the ocean at abyssal depths. The common widespread counterpart at slope and lower abyssal rise

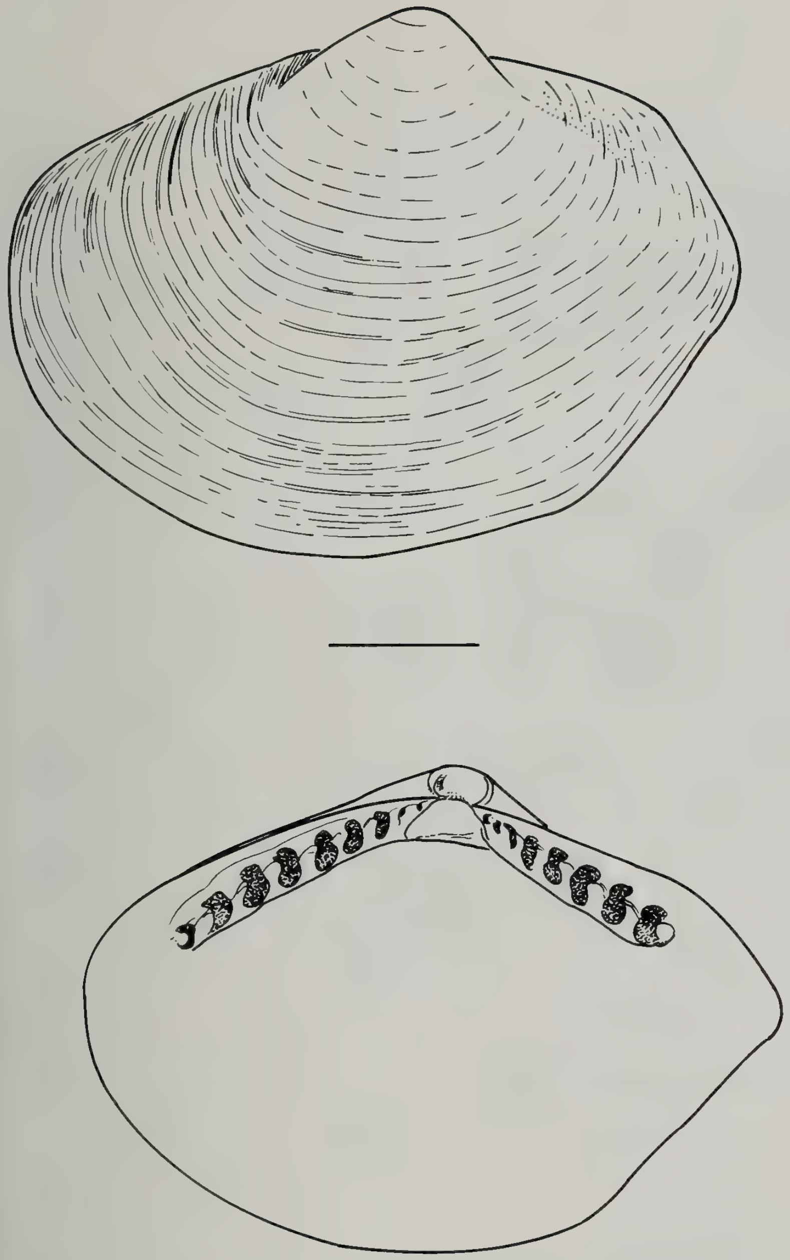

Fig. 79 *Ledella sp.*: Left lateral external view of shell of the specimen from Station 123 and lateral internal view of right valve of specimen from Station 83 to show hinge detail. (Scale = 1 mm).

depths is the *L. pustulosa* complex. This latter species appears to be in the process of speciation and here we recognise four closely related subspecies. Two, *L. p. pustulosa* and *L. p. marshalli*, while overlapping latitudinally in the North East Atlantic, are allopatric occurring on the slope abyssal rise and the upper abyssal depths respectively, the other subspecies, *L. p. argentina* and *L. p. hampsoni*, are geographically separate at abyssal rise depths. *L. modesta*, another common and widespread species, occurs somewhat deeper than the *L. pustulosa* complex. From these examples it is possible to make some general conclusions about the distribution of *Ledella* in the Atlantic and, from experience, also apply generally to the protobranch bivalves of the deep sea.

1) that common truely abyssal species are widespread in their occurrence.
2) common species of the slope and abyssal rise show sufficiently discernable population differences in shell form to an extent that true subspecies may be recognized.
3) rare species of the slope appear to have restricted distributions.

Occasional exceptions can be found to these general rules. Thus, *L. jamesi* common in the Argentine and Guinea Basins does not occur to the north and to the east. Such a distribution is known from other protobranch groups (Allen & Sanders in m/s, Sanders & Allen, 1965). In addition the benthic slope and abyssal bivalve faunas of the Argentine and Guiana Basins tend to have a high degree of endemism, but, unlike the impoverished fauna of Norwegian basin which also has a high degree of endemism, the isolated fauna off the East coast of South America is relatively rich in species. This is possibly correlated in some way to the north moving, relatively organically rich bottom water.

MORPHOLOGICAL EVOLUTION

Comparison of the specific morphologies of shells and various body organs shows that in common with most deep sea protobranch genera, the shell of *Ledella* is conservative in form with little variation in outline and sculpture. Similarly, with the exception of the configuration of the hind gut, there is little variation in the morphology of the viscera and such as there is, eg. adductor muscle size, can usually be related to other parameters such as the strength of the hinge and the size of the ligament.

The configuration of the hind gut in *Ledella* has considerable evolutionary significance. The various species of *Ledella* exhibit all the major hind gut configurations that are present in nuculanoid protobranch bivalves in general. The configurations are a consequence of the lengthening of the hind gut and the need to accommodate it in limited body space in the most advantageous way. The primitive nuculanoid condition is a single loop to the right side of the body. This is seen in three of the rarer species, namely *L. sandersi, L. similis* and *L. verdiensis*. All are from the East Atlantic at mid slope or abyssal rise depths. Modification of this configuration appears to take two forms. In one the loop of the gut extends to the left side of the body via the space between mouth and the posterior face of the anterior adductor muscle. On the left it may (*L. galathea, L. solidula, L. acuminata*), or may not (*L. oxira*), coil upon itself. In the other form, there is a loop *first to the left* and then to the right side of the body crossing to each side posterior to the stomach. (*L. pustulosa, L. modesta, L. jamesi* and *L. lusitaniensis*). Species exhibiting these two main types of configuration are found throughout the Atlantic from upper slope to abyssal depths. Finally, there are two species which have other configurations. In the case of *L. ultima* the hind gut has multiple coils on the right side of the body. This, like loop extended to the left and there coiling, is easily derived from the primitive condition by coiling the single loop several times (Fig. 81). This configuration is also typical of many species of *Spinula* (Allen & Sanders 1982) and seems to be particularly associated with those species living at abyssal depths. It is a device that simply ensures the maximum extension of the gut within a limited volume of body space. One further condition, to date found only in *L. parva*, is two loops to the right and one to the left. This too can be derived from the primitive condition, the first loop to the right being the proximal part of the hind gut. *L. parva* has a restricted distribution on the upper slope of the East coast of the United States and, for an upper slope species it has an extremely long gut.

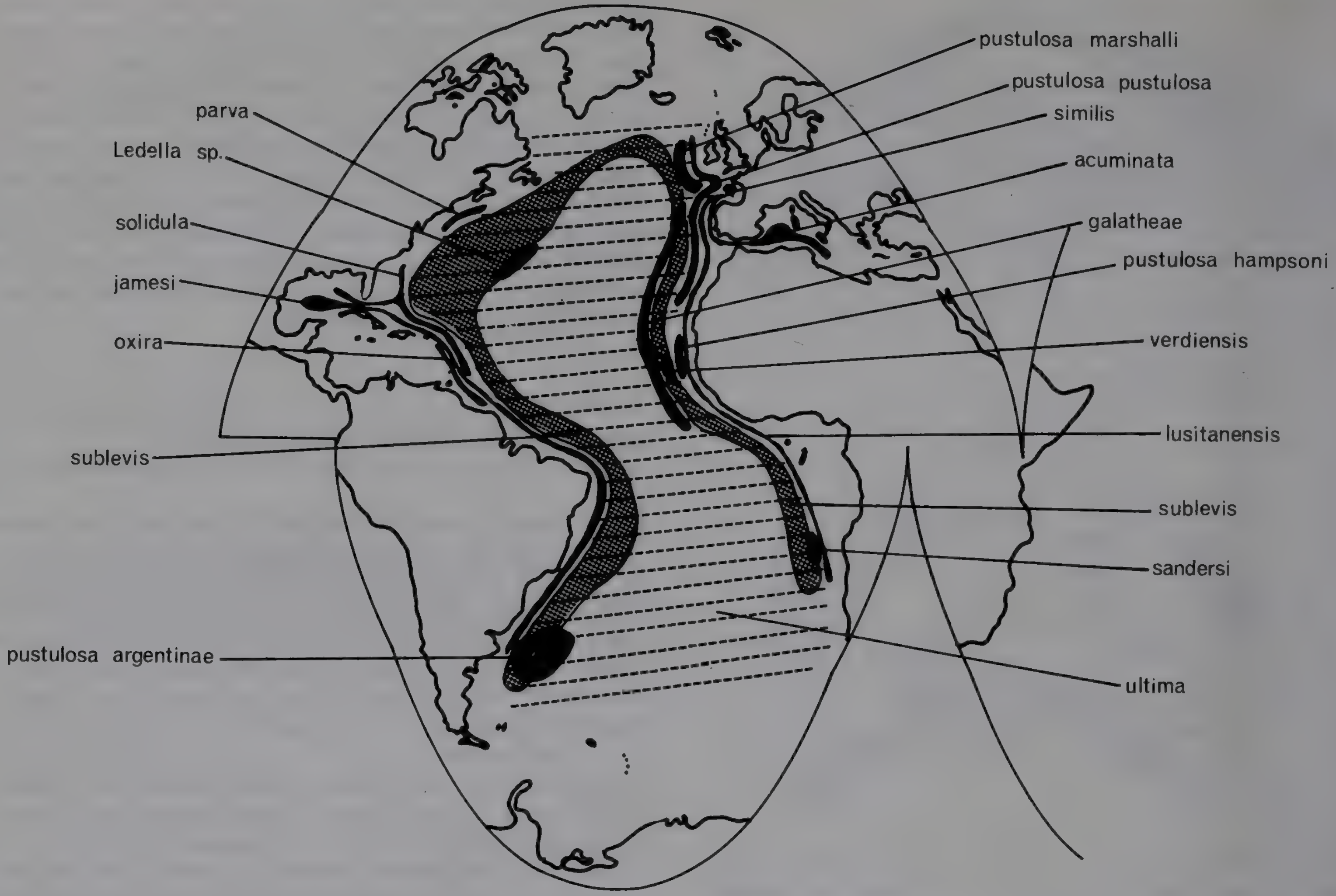
parva
Ledella sp.
solidula
jamesi
oxira
sublevis
pustulosa argentinae
pustulosa marshalli
pustulosa pustulosa
similis
acuminata
galatheae
pustulosa hampsoni
verdiensis
lusitanensis
sublevis
sandersi
ultima

Fig. 80 The distribution of the *Ledella* species in the Atlantic.

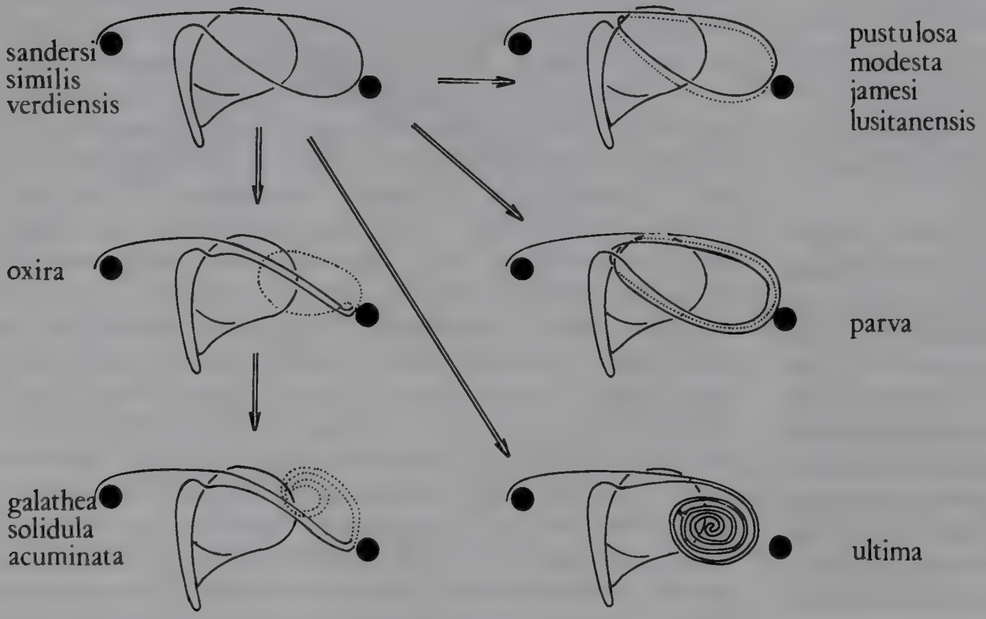
sandersi
similis
verdiensis
pustulosa
modesta
jamesi
lusitanensis
oxira
parva
galathea
solidula
acuminata
ultima

Fig. 81 The radiative evolution of hind gut configurations in species of *Ledella*.

Thus, the length of the hind gut and its relationship to the depth at which its possessor lives is not entirely consistent. Species possessing a short single loop are not all found at slope depths, but in general most abyssal species have long hind guts. Conversely elongate hind guts can be found in a few upper slope species and presumably give digestive advantage.

In a small species an enlarged gut has the disadvantage of restricting the space for gonadial development but then food reserves are in such short supply in deep water as to limit egg production. Presumably there is a fine balance between energy supply and space apportionment. In this regard adaptive advantage would appear to be in the exceptional change of direction of shell growth as seen in *L. ultima* and with the consequent enlargement of shell space. *L. ultima* is certainly the numerically and geographically the most successful species of the subfamily.

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Manuscript accepted for publication 2nd November 1988

Bull. Br. Mus. nat. Hist. (Zool.) **55** (2) 173–207 Issued 26 October 1989

Systematic account of a collection of fishes from the Mongolian People's Republic: with a review of the hydrobiology of the major Mongolian drainage basins

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INTRODUCTION

The Mongolian People's Republic (MPR) occupies over one and a half million km^2 of high, central Asia. Zoogeographically, this is a unique position as the country encompasses within its borders part of the three major Central Asian drainage systems; the Arctic, Pacific and Central Asian Internal basins.

Despite the country's unique position, the fishes of Mongolia are poorly known. Original descriptions by Russian and Mongolian authors and other references in the scientific literature are widely scattered and often inaccessible, particularly to western scientists.

It is hoped that the publication of a series of volumes entitled '*The Vertebrates of the Mongolian People's Republic*' of which the first two were devoted to fishes (Shatunovskii, 1983 & 1985; issued in Russian) will improve this situation. A proposal for the translation of these volumes from the original Russian into English, has been submitted to the Smithsonian Institutions Library, Translation Publishing Program.

Historical review

The earliest collection of fishes known from Mongolia was made by the German naturalist Peter Simon Pallas (1774–1811); see Cuvier (1819) for a discussion of his scientific activities.

Pallas undertook his pioneering travels through eastern Russia and Siberia during his tenure of the Chair of Natural History at the St. Petersburg Academy of Sciences (Svetovidov, 1981). From the valuable collections of skins and alcohol-preserved specimens sent back to St. Petersburg from Mongolia he was able to describe the salmonids *Hucho taimen* (Pallas, 1773), *Brachymystax lenok* (Pallas, 1773), *Thymallus arcticus* (Pallas, 1776) and cyprinids *Hemibarbus labeo* (Pallas, 1776), *Rhodeus sericeus* (Pallas, 1776) and *Pseudaspius leptocephalus* (Pallas, 1778).

Exploration of this region was continued during the last century, notably by Dybowski (1869, 1872 & 1876), Basilewsky (1855), Kessler (1878) and Warpachowski (1889); their work included the description of many new species.

The start of this century saw the first of numerous studies on the fishes of the region by Berg (e.g. 1909), which

Fig. 1 Professor Anudarin Dashdorzh (1910–1976)

eventually led to his classic monograph on the *Freshwater Fishes of the U.S.S.R. and Adjacent Countries* (Berg, 1916; original edition in Russian). This work has passed through four editions and remains the standard reference to the majority of fishes from Mongolia despite the recent publications discussed above.

The founding in Ulan Bator of the Mongolian State University (1942) and the Institute of Biology of the Academy of Sciences (1965) greatly increased local research on the rich fauna of the country's lentic and lotic aquatic environments. The first Mongolian to hold the Chair of Zoology, Professor A. Dashdorzh (Fig. 1) had a particular interest in the fishes of his native land (e.g. Dashdorzh, 1955 & 1962; Dashdorzh, Dulma & Pivnička, 1963; Dashdorzh & Tomilov, 1965).

The first expedition to be organised from the west occurred during the first half of this century with the First, Second and Third American Museum of Natural History Asiatic Expeditions. These spent several summer months between 1922 and 1930 in the south and western Gobi. A small collection of fishes was obtained by Roy Chapman Andrews and his colleagues; they recognised two distinct forms of *Oreoleuciscus* from isolated Gobi basins (Andrews, 1932: 121 & 298). This material was briefly mentioned by Nichols (1930), but it has never been fully described and was beyond the scope of his monograph '*Freshwater Fishes of China*' (Nichols, 1943: V).

Since the time of these multidisciplinary expeditions to the Central Asian Internal basin, and a small region of the Arctic basin (Andrews, 1932: 54), only a few specimens have been received by western museums and institutions concerned with taxonomic research (e.g. British Museum [Natural History]). There have been no other expeditions from the west and none solely devoted to the study of Mongolian fishes, until that reported upon here.

Recent times have seen joint Soviet-Mongolian (1946 & 1948–9 and from 1970 to the present), Polish-Mongolian (1962–1965 & 1967–1971), Czechoslovakian-Mongolian (1966) and German Democratic Republic-Mongolian (1964–1970) collaboratory scientific field studies. However, these have tended to concentrate on geological, palaeontological or broad multidisciplinary biological studies (Vasil'eva, 1985 and see listings for Mongolia in *Bibliography and Index of Geology* from 1969 to date). They have contributed to our understanding of the taxonomy of some species, by providing new collections of fishes for analysis by ichthyologists in the countries concerned (e.g. Holčik & Pivnička, 1968; Chitravadivelu, 1970).

Collecting strategy

The bulk of the ichthyological fieldwork in Mongolia extended from 7 August to the 5 September 1984. It was restricted to 10 principal localities (numbered on Fig. 2), partly due to the geographical and political isolation of many regions (especially the border areas), and because transport and fuel were in such short supply.

The major objective of the survey was to collect samples and comparative ecological data from waters in each of the three distinct drainage basins. To achieve this with the limited facilities available, the field programme consisted of two main components; a three week expedition west of Ulan Bator to visit sites in the Arctic and Central Asian or Internal drainage basins, and a single week's expedition east of the capital to visit a further locality with Arctic drainage as well as the major Mongolian river system in the Pacific drainage basin.

Materials and methods

A Russian built Gaz 69 Jeep and coupons for 400 litres of diesel fuel were provided by the Mongolian Ministry of Transport, together with a driver/mechanic. A member of the Biology Department at the Mongolian State University acted as local guide and interpreter.

Collections were made with sinking and floating gill nets of mesh sizes ranging between 1–10cm; these were employed extensively. Rotenone, beach seine and dip nets were used if suitable conditions prevailed. Water salinity was measured with a portable conductivity meter and the water clarity in the two lakes with the aid of a Secchi disc which was also used to measure depth. The temperature of the water was read from a suspended mercury thermometer. The elemental compositions of the salt samples taken from the margin of an isolated water body of Boon Tsagaan Nuur (Nuur = Lake) in western Gobi were determined with a Jerrell-Ash Model, 750 Atom-Comp direct reading ICAP (Inductively Coupled Argon Plasma) Spectrophotometer, using dilutions of Fischer Scientific absorption stocks for standards. The English spelling of place names follows that generally adopted in scientific publications, or from maps in Bartholomew's World Travel Series and British Ministry of Defence Operational Navigation Charts (ONC E7–8 & F7–8)

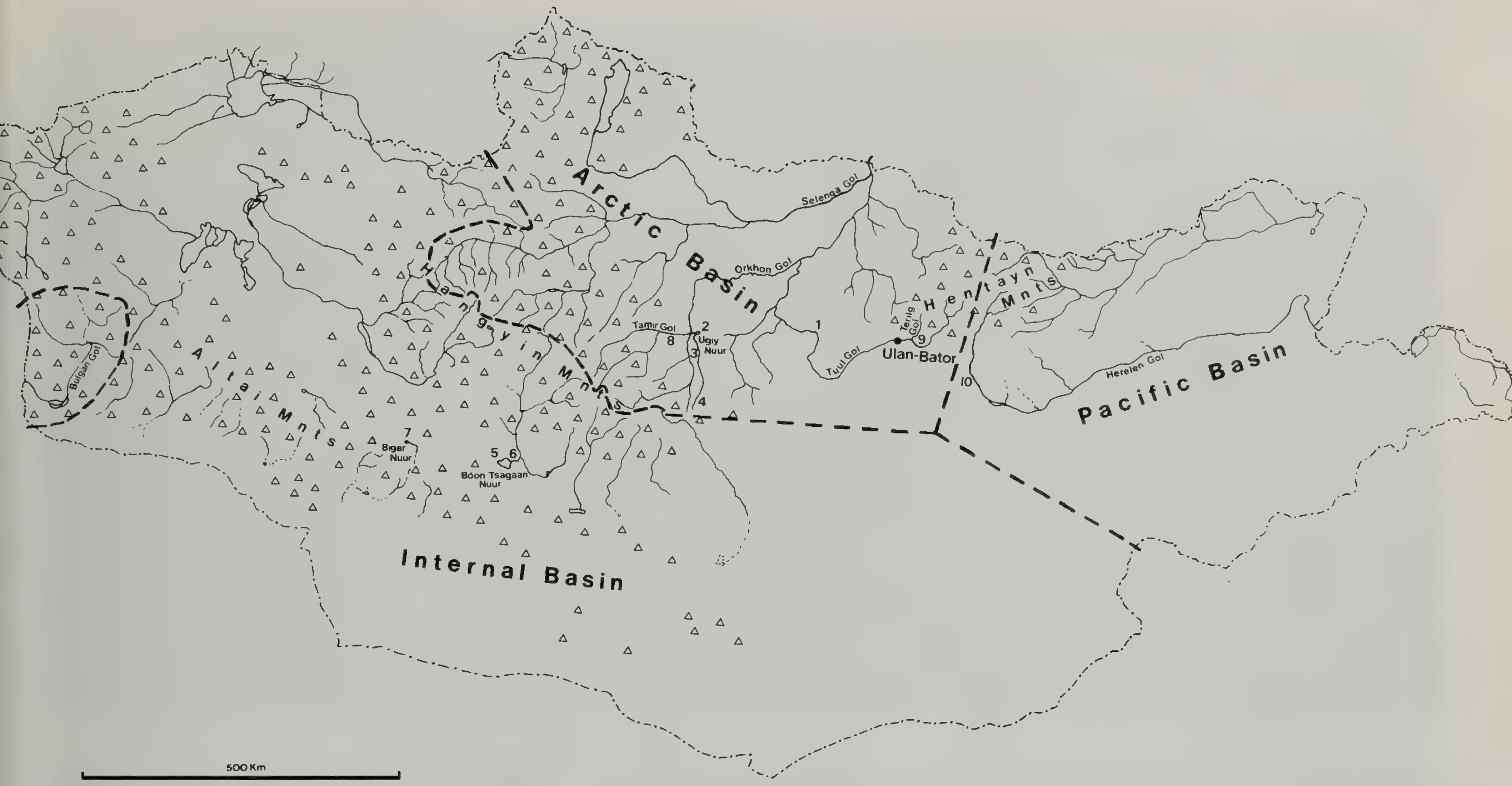


Fig. 2 Map of the Mongolian People's Republic to show major mountain ranges (△), rivers (=Gol) and lakes (=Nuur). The three main drainage basins are outlined and the principal collecting localities are numbered: 1. Tuul Gol; 2. Ugiy Nuur; 3. Orkhon Gol; 4. Hogshin Orkhon Gol; 5. Boon Tsagaan Nuur; 6. Tsagaan Gol; 7. Biger Nuur; 8. Tamir Gol; 9. Terilg Gol; 10. Herelen Gol.

HYDROBIOLOGY OF MONGOLIA

Past conditions

Mongolia lies in the mountainous central Asian plateau that is a geographical transition zone between the Siberian taiga and dry steppe and desert of central Asian Gobi (Mitcheli, 1967; Petrov, 1970; Jagchid & Hyer, 1979; Saunders, 1987).

The origin of Mongolia's present-day hydrobiology can be traced back to the Cretaceous (Berkey & Morris, 1927; Martinson, 1955). In the lower Cretaceous, an enormous inland lake had widened to the north as a continuous system connecting what are now the disparate Altai and Hangyin basins, and formed inner basins of the type found in Recent times around the Aral and Caspian seas (Dulma, 1979). This continuous lake system is thought to have extended by the middle Cretaceous from what is now the Pacific eastern seaboard across Manchuria and Central Asia into the western Gobi basin of Mongolia (Fig. 2). Geological studies (e.g. Maleyev, 1955 and Martinson, 1968) reveal that a large central Asian freshwater system existed in the upper Cretaceous. This was responsible for sedimentary deposits rich in palaeontological remains. Grabau (1931), Andrews (1932), Kielan-Jaworowska & Dorchin (1968) and Kielan-Jaworowska & Barsbold (1972) described primitive mammals, dinosaurs and other reptiles from the shores of this system; for recent reviews of Mongolian Paleogene deposits see Russell & Zhai (1987) for mammals and Sytchevskaya (1986) for fishes.

This great central Asian basin is thought to have broken-up by the end of the Cretaceous. The modern topography was then shaped by alpine orogenesis at the end of the Pleistocene (Petrov, 1976).

These tectonic movements produced the three mountain ranges that dominate the local scenery (i.e. Altai, Hangyin and Hentayn). Their folding and subsequent shaping are the chief factors responsible for the present-day hydrographical network of the region.

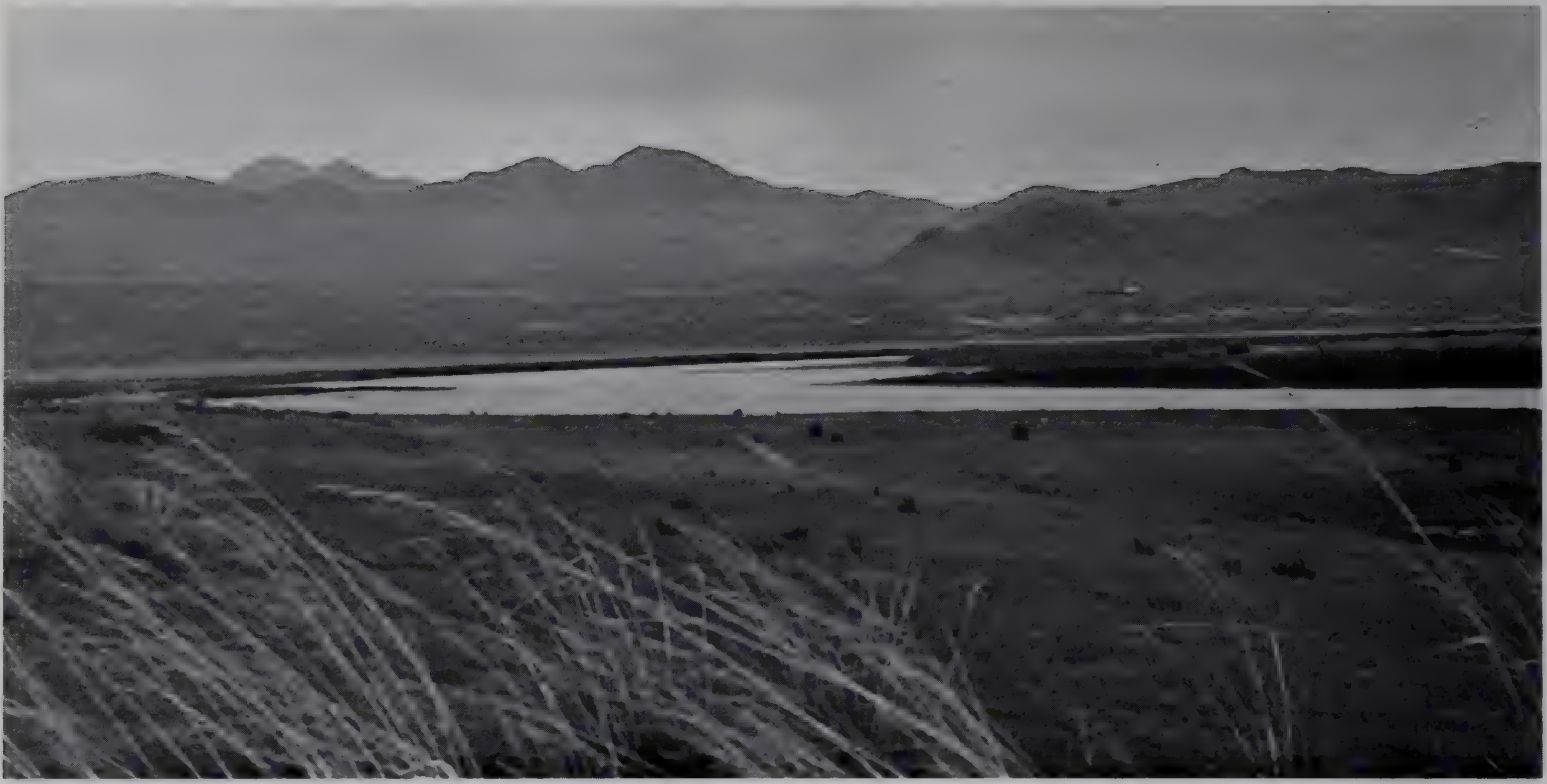
The drainage basins within the borders of the MPR are clearly defined by the mountain ranges that subdivide the country (Fig. 2). Four of the zoogeographical subdivisions of the USSR and adjacent countries defined by Berg (1948) extend in part across the territory of Mongolia. Three of these were considered by Berg (1948, coloured map) to lie within the Holarctic region. They consist of the Arctic province, within his Circumpolar subregion, and the West Mongolian and Tarim provinces, in his Asiatic Highland subregion. The fourth Mongolian faunal region defined by Berg (1948) is the Amur province, within his Amur Transitional region. His analyses relied solely upon comparison of fish faunas from distinct water bodies and drainage basins in these areas.

More recent comparisons between the aquatic faunal compositions of Mongolian zoogeographic provinces based largely on planktonic and ichthyological surveys (Dulma, 1979; Shatunovskii, 1983; Dgebuadze, 1986), suggest Berg's Tarim and West Mongolian provinces should be united zoogeographically even though they are now hydrologically isolated. Evidence from recent tectonic reconstructions of the area support their amalgamation.

Present drainage systems

Arctic Basin

The Mongolian part of the Arctic province consists of three major river systems with associated lakes and tributaries; the Bulgan, Shishlid and Selenga. Together they have a total



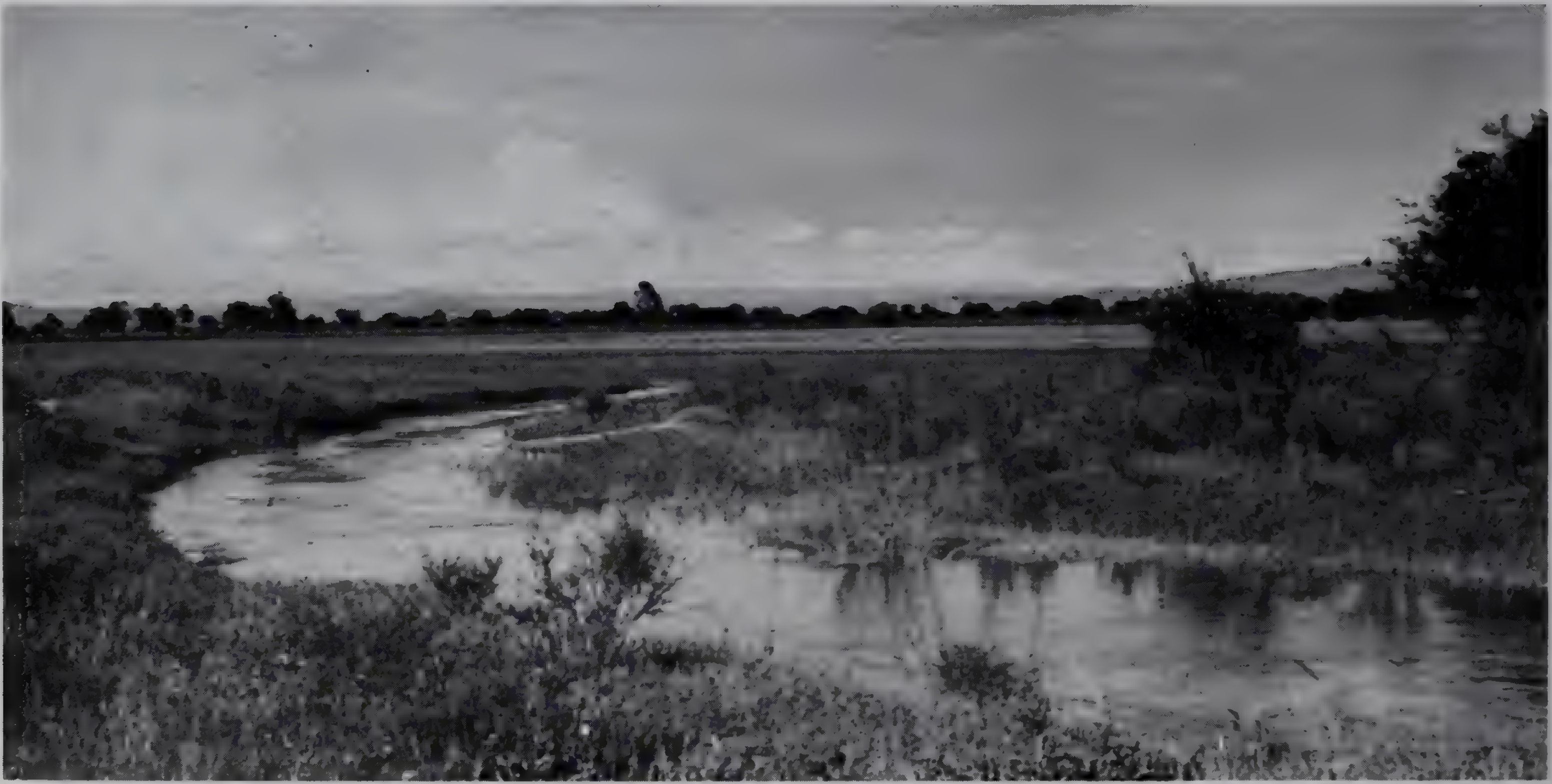


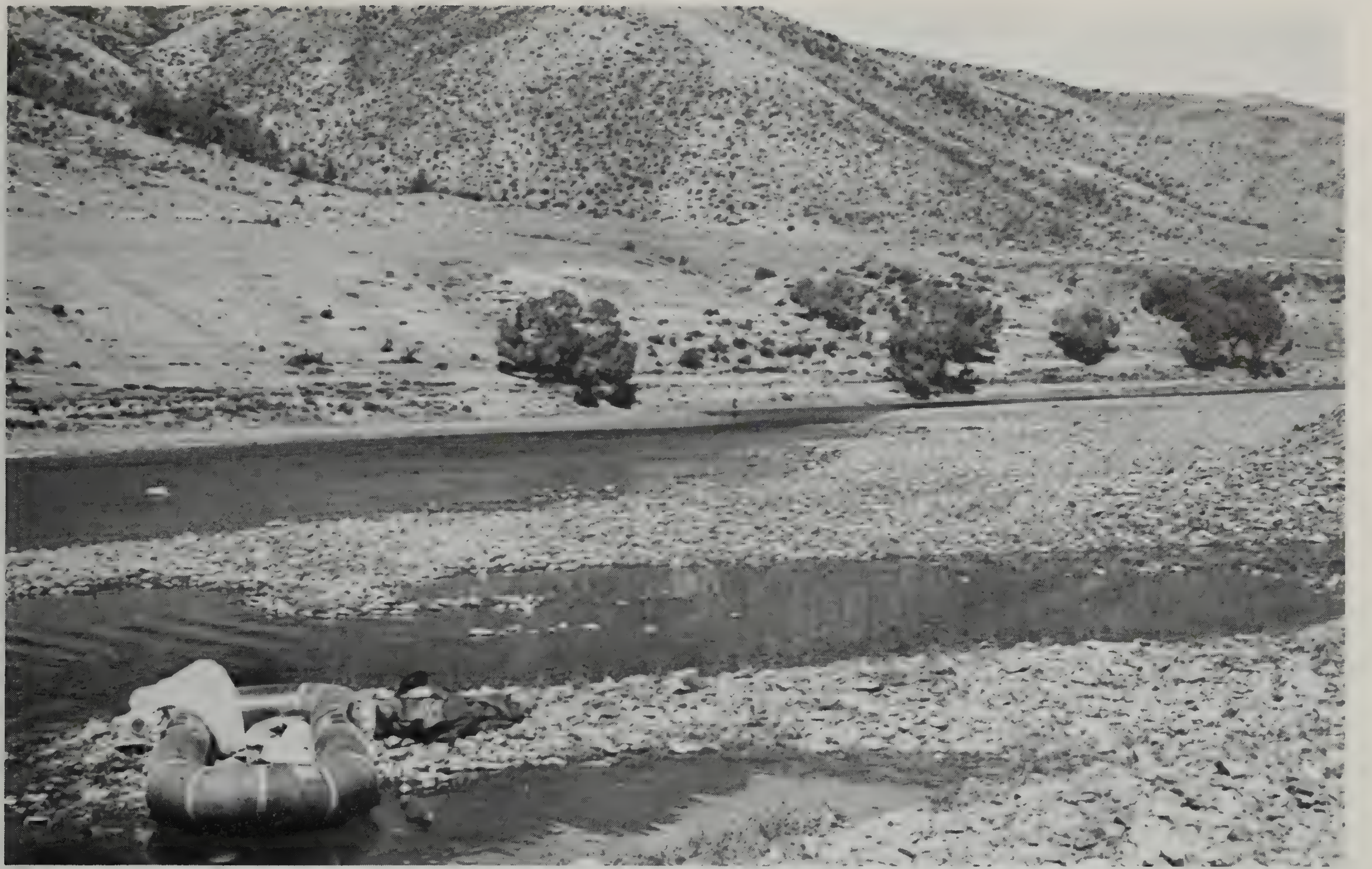
Fig. 3 Principal collecting localities; (Above) Tuul Gol, 5 km north of Lun and (Below) Tamir Gol, 2–3 km upstream from confluence with upper reaches of Orkhon Gol.

catchment area of 323,000 km^2 or 20.6% of the whole country (Dulma, 1979).

The Bulgan River system drains the southern slopes of the Altai mountain range. It is separated from the other part of the Mongolian Arctic basin by the western Gobi valley. These waters support a fauna that is almost indistinguishable, although the Bulgan River now empties into Lake Ulungur Province (People's Republic of China) which has no outlet and is an enclosed system (endorheic). The isolation of this system may have occurred during uplift of the Altai mountain range which divided the Central Asian basin (discussed below).

The Shishlid River system is a relatively short headwater of the Yenisei River and occupies the most northern tip of Mongolia, just west of Khbsugul Nuur.

The Selenga River system is the largest in the Mongolian Arctic basin; it encompasses 87.3% of the basin, has a drainage area in excess of 280,000 km^2, a total length of about 1,500 km and supplies 50% of the affluent of Lake Baikal (Kozhov, 1963). The Selenga's tributaries consist of many large rivers and lakes (e.g. Terilg, Tuul, Orkhon & Tamir Gols and Khbsugul, Terhiyn and Ugiy Nuurs). It is the principal headwater of the Yenesei River which courses across Siberia before eventually emptying into the Arctic Ocean.



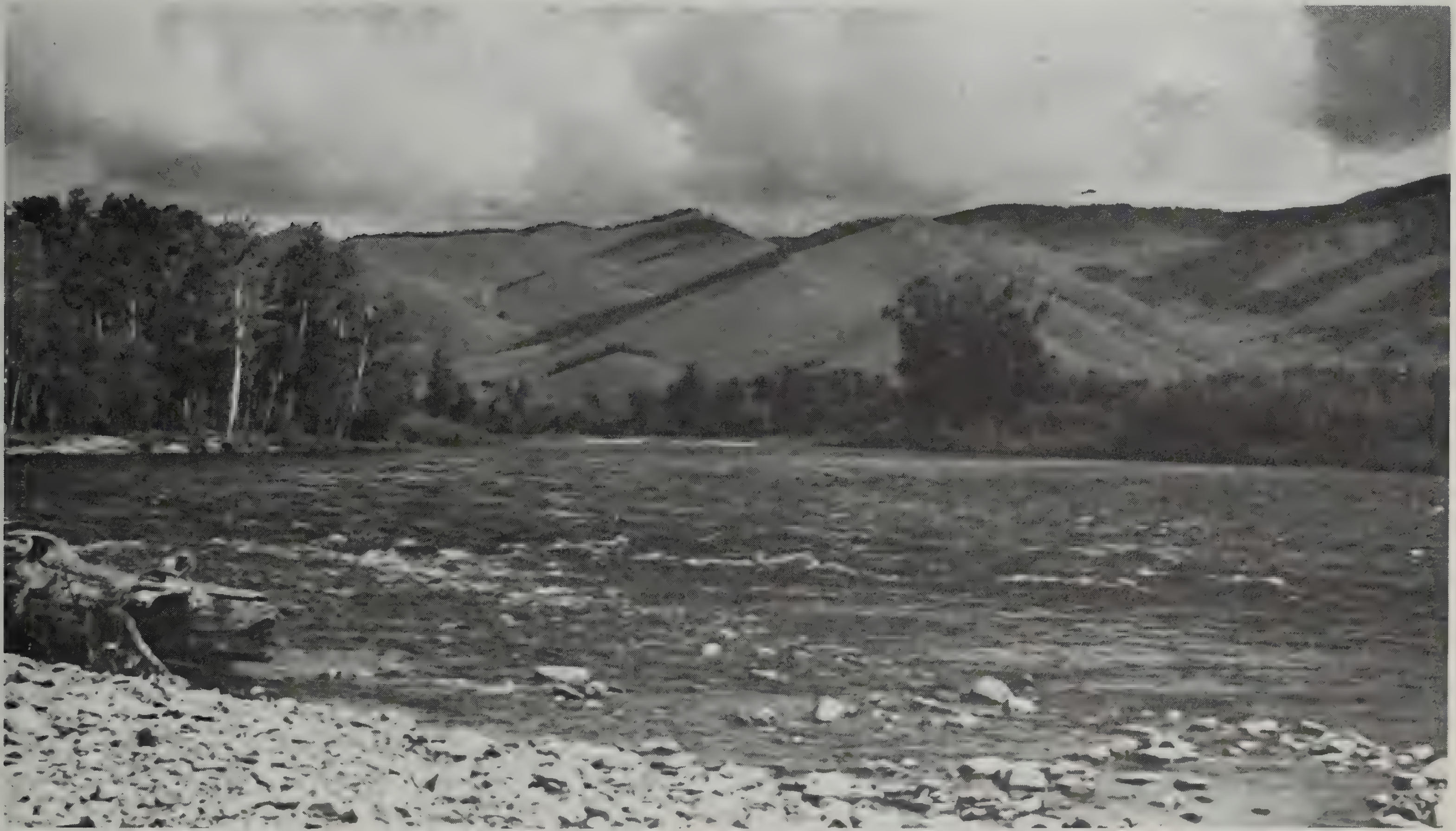


Fig. 4 Principal collecting localities; (Above) Orkhon Gol, 1 km upstream from bridge at Harhorim (Karakorum) and (Below) Terilg Gol, at end of vehicle track 35 km east of Ulan Bator.

The six principal Arctic basin localities visited during the course of my survey were all confined to the Selenga system. They consisted of five rivers and one lake. The rivers sampled in this northern basin fall into three types: 1) medium level with slow current, deep turbid water over a detritus covered substrate, supporting dense macrophyte growth (e.g. Tuul

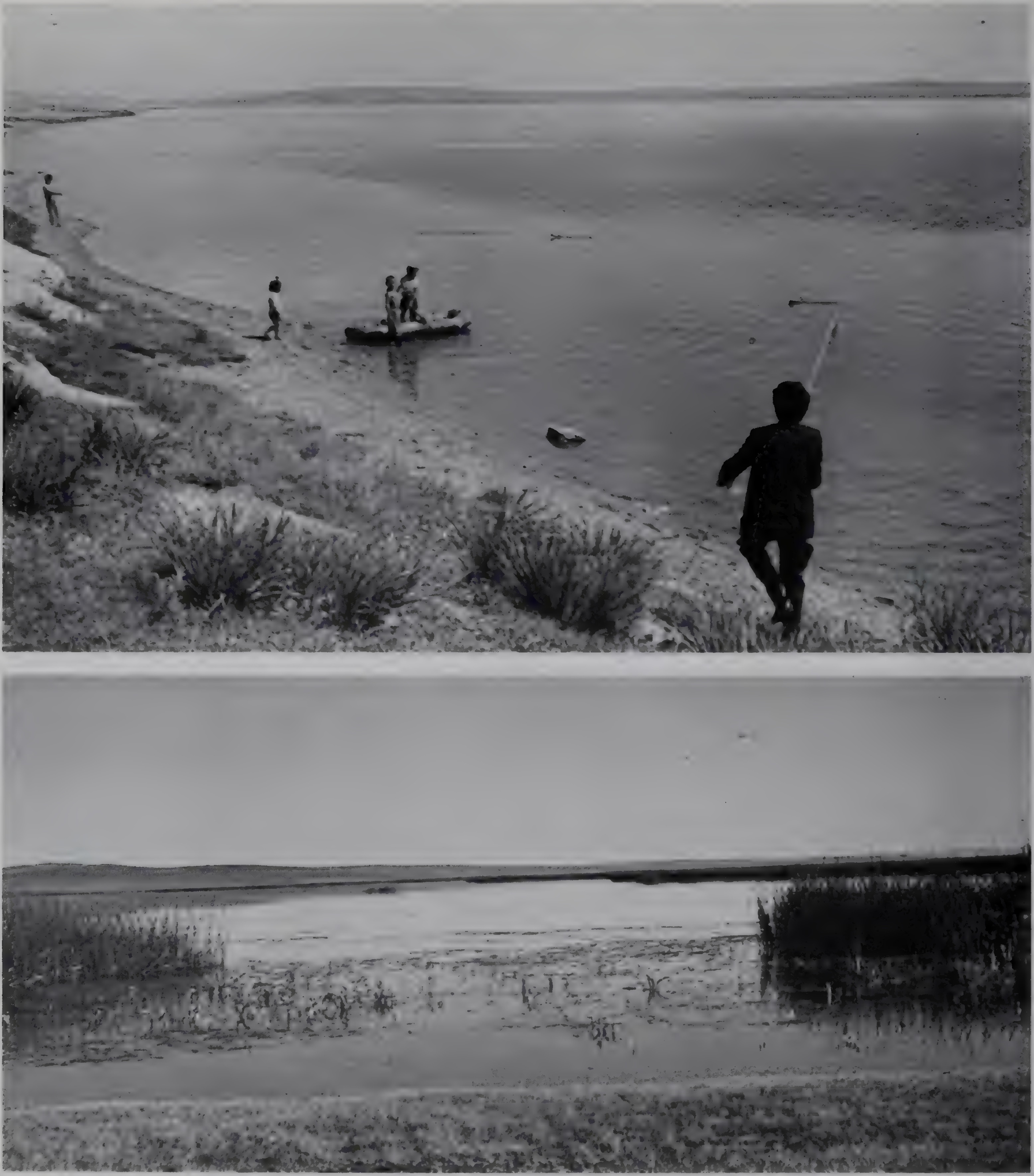


Fig. 5 Principal collecting locality Ugiy Nuur, 1 km west of outlet into Orkhon Gol. (Above) Beach seining along southern shore and (Below) swamp region prior to outlet into Orkhon Gol.

and Tarim Gols: Fig. 3); 2) high altitude 'salmon rivers' (Odum, 1978: 298) with fast flowing, clear water over a stony, gravel substrate with little rooted aquatic vegetation (e.g. Orkhon and Terilg Gols: Fig. 4); and 3) narrow head-water streams that course across high altitude alpine meadows and consist of deeper pools and riffles (e.g. Hogshin Orkhon Gol: Fig. 2 locality 4). Generally they have grassy banks and wide flood plains, with small rivulets and ponds. The water level was often high, with increased current and flooding at several localities. This was due to the high precipitation during the months of July and August in northern parts of Mongolia (Petrov, 1970). The sparse vegetation allows rapid run-off which results in dramatic changes in water level following short but heavy periods of rainfall.

The only lake sampled in the Selenga system was Ugiy Nuur (Fig. 5). It is an elongated mesotrophic lake covering an area of 2.5 km^2 and appears to have been formed by the dislocation of the Orkhon Gol in a shallow valley on the northern margin of the Hangyin mountain range (Fig. 2; locality 2). Its greatest depth is 16 m and water transparency 3 m. Clear, shallow water constitutes 40% of the total lake area and it is thought about 50% of the lake bottom supports macrophytic plants (Dulma, 1979: 716 and *pers. obs.* underwater).

Rooted macrophytes were found to be particularly dense in the effluent region of the lake; large predatory species (e.g. *Esox*) were common in this area. Dulma (1979) considered the lake to be ichthyologically a 'roach-pike type' and listed its 'useful fish species'.

Pacific Basin

The major lentic waters of the Mongolian Pacific basin consist of Buyr and Holi Nuur, the principal lotic waters are the Onon Gol, Herelen Gol, Halhin Gol and Uldra Gol. The Herelen Gol is the largest river and runs 550 km from its source in the Hentayn mountains to Dalai Nuur. This river together with the Onon, forms the Mongolian headwaters of the Amur River system which eventually flows into the Sea of Okhotsk and the Pacific Ocean. The connection of the Herelen with the upper reaches of the Amur is subject to seasonal fluctuations. Dalai Nuur (Hu-lun Ch'ih) is bound by marshland to the east and north of the lake. A series of pools may become interconnected at periods of high water and form a link between this lake and a southern branch of the Amur's headwaters (Hailar Ho River).

The single Pacific basin locality visited during the course of this survey was along the Herelen Gol, about 60 km downstream of the main bridge in Kentei Aimak (see below). Several sites were extensively sampled and include the main river, many rivulets running across the marshy flood plain, and some isolated ponds (see p. 189 and Fig. 6). The main body of the river at this point is in excess of 50 m wide and was in spate following the heavy precipitation of the previous month.

The strong water current had disturbed the relatively high level of benthic debris and the water was turbid (Fig. 6). Young willow trees grow along the low muddy river banks and contribute allochthonously to the productivity of this stretch of the Herelen Gol; no other trees exist in this region. The flood plain on the west bank of the river is about 1 km wide and consists of a wide water meadow supporting, during the summer months, a large variety of grasses, flowering plants and insects. The many rivulets or streams that wind across these plains have a slow current of clear water and support a dense community of rooted macrophytes. Small isolated ponds (about 20 m in diameter with maximum depth of 2 m) occur along the streams and maintain a dense flora of aquatic macrophytes in their clear waters and peripheral clumps of reeds (Fig. 6).

Central Asian Internal Basin

The independent central Asian basin consists predominantly of large lentic water masses without outlets beyond this basin. They are fed by relatively short upland streams or rivers that drain the southern slopes of the Hangyin and northern slopes of the Mongolian Altai mountain ranges. Although these waters share a common fauna (see p. 193), geomorphologically the basin can be subdivided into the west Mongolian Great Lakes Valley and Gobi Valley Lakes (Dulma, 1979; Dgebuadze, 1986). The former includes several mountainous lakes and streams on the northern slopes of the Gobi Altai (e.g. Orog Nuur) and Hangyin Plateau. These ranges contain some of the highest mountain lakes in the country, with water levels varying in elevation from 759 m to 2232 m (Dulma, 1979: 714). All of these closed drainage systems eventually terminate in large endorheic lakes. The high concentration of dissolved salts (discussed below and see Table 1) often causes a white precipitate to occur around the lake margins. Some freshwater lakes are present (e.g. Archit Nuur in the Altai and Hungiiyn Har Nuur in the Hangyin mountains) but their outlet streams ultimately flow into an endorheic lake. The freshwater lakes are generally elongate and originated through karst formation. Despite the topographical distortions and rearrangements of the hydrographical network within the Central Asian basin, it retains a uniform fauna (Sokolov & Semyonova, 1986).

The principal localities sampled during the course of this survey in the Central Asian basin were Boon Tsagaan Nuur and its inflowing freshwater stream Tsagaan Gol, a tributary of Baydarag Gol (Fig. 7). In addition to this locality specimens were also obtained from Biger Nuur (discussed below). Both these lakes lie within the intermontane basin separating the Hangayn and Gobi Altai mountains which extends in an east–west direction for nearly 350 km (Fig. 2).

Boon Tsagaan Nuur is a deflation lake and typical of a series of permanent and seasonal endorheic lakes found in the western Gobi (Fig. 8 and see Davies, 1986). It has no outflow; several small streams and springs flow into the lake, the largest is Tsagaan Gol, an arm of Baydarag Gol which originates from the Hangyin highlands.

The presence of a series of ancient raised beaches clearly indicates that in the past this lake was of much larger proportions (Fig. 8); they were originally discussed by Andrews (1932: 300). To support a larger water mass, the carrying capacity of the inflowing river must have been far greater than the present Baydarag Gol system which is little more than a highland stream of clear, medium fast flowing water, with only dissolved sediments held in suspension. The eastern, isolated sub-basin of Boon Tsagaan Nuur (Fig. 8) does not appear to have any inflowing waters and is developing towards a dessicated salt-pan.

At present the shrinking of Boon Tsagaan Nuur, shown by the height and number of its raised beaches, appears to be in a continuing phase (this observation was supported by discussions with local inhabitants who described a lake of much larger proportions known to earlier generations).

Raised relict beaches are common around other basins in the Gobi Valley (e.g. Tsatsin Tsagaan Nuur, see Berkey & Morris, 1927: 247 & 392–3). Andrews (1932: 277) described '. . seven ancient beaches, high above the water level of 1922' off Tsatsin Tsagaan Nuur. The origin of the deflation basin that gave rise to the present lakes and the past higher water levels, led these authors to conclude that past climatic conditions must have been more arid or humid than at present. These unstable climatic fluctuations do not appear to have occurred gradually over a continuous period but in cycles or punctuated phases.

The salinity of the lake's water is not simply due to evaporation exceeding precipitation in this semi-desert region. The high concentration of dissolved ions in Boon Tsagaan

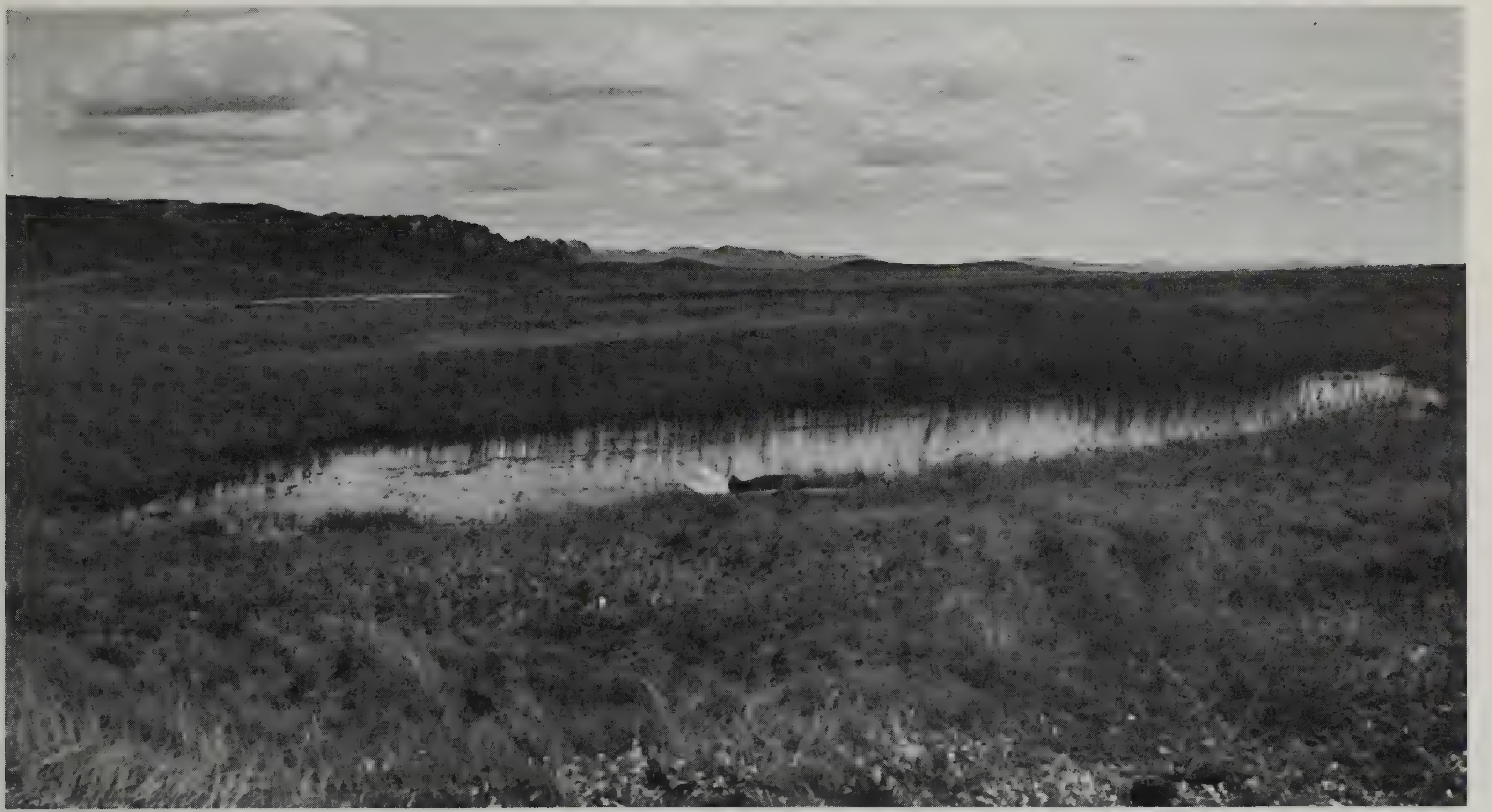


Fig. 6 Principal collecting locality Herelen Gol, 60 km downstream of bridge in Kentei Aimak, western bank. (Above opposite) Willow shoots along side channel, (Below opposite) main river in spate and (Above) isolated pond in flood plain.

Nuur is shown by the conductivity readings given below (p. 187).

In drying pools an evaporate is produced which can be several centimetres thick (Fig. 8), it supports a dense growth of salt tolerant *Salicornia*. Analyses of the evaporate revealed, not unexpectedly, a high concentration of calcium, magnesium, sodium and potassium; the concentrations of these and other elements in samples from two sites are summarised in Table 1. The high levels of these elements may be directly related to intense photosynthesis occurring in the lake (Goldman & Horne, 1983), the geological composition of its watershed and the absence of an outlet which will cause the lake to accumulate ions even if it is not contracting.

Table 1 Element concentrations (μg/g fresh weight) in salt samples from two sites around shore of isolated water body off Boon Tsagaan Nuur.

Element	Dist.H_2O	Sample 1	Sample 2
A1	.0234	.0568	.0225
B	.0062	1.2978	9.9068
Ca	.0209	41.4791	1.5461
Cd	.0027	.0029	.0021
Co	.0019	.0032	.0033
Cr	.0023	.0374	.0171
Cu	.0901	.0109	.0151
Fe	.0138	.0056	.0000
K	1.1680	10.1220	157.9320
Mg	.0087	62.3513	29.2913
Mn	.0004	.0032	.0019
Na	.1881	768.9119	786.2119
Ni	.0471	.0441	.0294
p	.0585	.7424	.3820
Pb	.0448	.0038	.0000
Si	.0073	.2946	.1956
Zn	.0152	.0116	.0070
Mo	.0261	.1197	.4533
Sr	.0000	2.2820	.6441
Ba	.0012	.0097	.0213

Elemental compositions were determined with an ICAP (inductively coupled argon plasma) spectrophotometer, using dilutions of atomic absorption stocks for standards.

Water clarity was low during August (see Secchi Disc readings given below p. 187). This is due to a massive algal and zooplankton bloom (autochthonous production). No macrophytes were observed along the wave washed littoral zone or even further offshore.

The water temperature of this holomictic lake was relatively high (see below) but dramatically dropped after a three day storm produced thorough mixing of the lake waters, which were otherwise prone to temporary thermal stratification. A massive development of zooplankton occurs in Boon Tsagaan Nuur during July and August (*pers. obs.* and Dulma, 1979: 728 gave average biomass as 2.1 g/m^3). The sandy substrate supports a rich fauna of zooplankton including rotifers, larval stoneflies (Plecoptera), dragonflies (Anisoptera) and caddis flies (Trichoptera).

Dulma (1979) classified the holo- and dimictic water bodies of the Gobi Valley as oligotrophic lakes. The productivity of saline lakes is often considered to be high (Goldman & Horne, 1983: 382), based on a few but nevertheless abundant species. The massive plankton bloom obtained during August, together with the high yield of fishes, suggests greater eutrophication than normally associated with oligotrophic systems. However, the sudden peak in productivity is short lived and must dramatically drop off to a much lower level during the

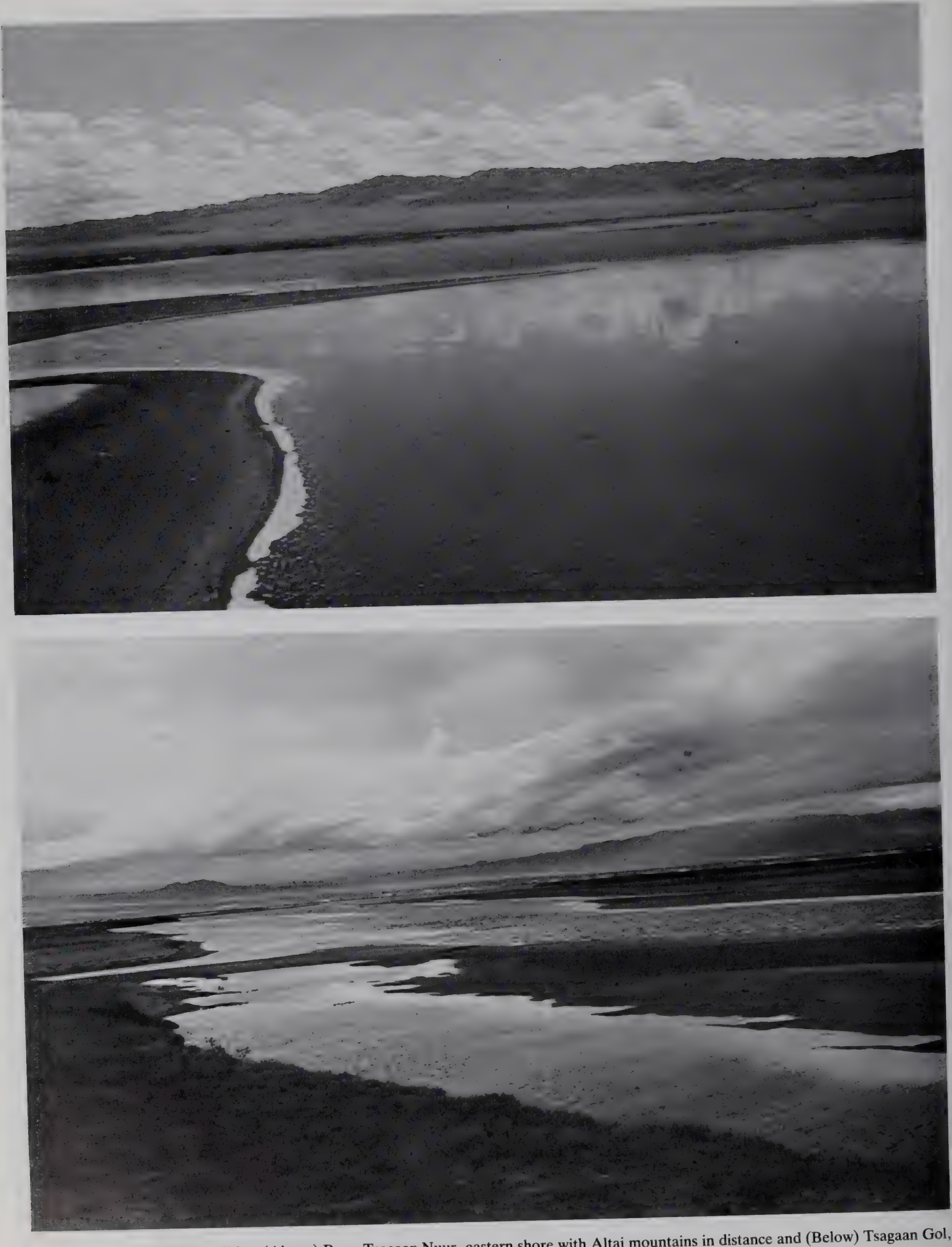


Fig. 7 Principal collecting localities; (Above) Boon Tsagaan Nuur, eastern shore with Altai mountains in distance and (Below) Tsagaan Gol, showing small inflowing tributary and outlet into lake.

severe winter months when between December and April the lake is frozen to a depth of 50–80 cm; this prevents mixing and thermal stratification must occur beneath the ice.

The low diversity of organisms in Boon Tsagaan Nuur makes it an ideal lake for productivity and food chain analyses.

Tsagaan Gol is a shallow stream (under 1 m) with a moderate current of clear, fresh water; its conductivity readings are given below (p. 187). The substrate consists of fine gravel with little interstitial benthic debris. However, a 2 cm mesh sized net strung across the stream soon became clogged with allochthonous plant debris which would normally be fed into the lake. Several small spring fed tributaries course across lake shore terraces to connect with Tsagaan Gol; rooted macrophytes and filamentous algae were common in these rivulets.

The width of the main stream is about 10 m, although it was several times this at its mouth into the lake (Fig. 7). On either side of Tsagaan Gol, around the north and eastern margin of the lake, are wide terraces covered in grasses and flowering plants. These are underlain by numerous freshwater springs as described around the shores of Kholoboldii Nuur by Andrews (1932: 288).

Biger Nuur and its inflowing stream Dzost Gol form an isolated basin draining the northern slopes of the Mongolian Altai mountains at the western end of the Gobi Valley, Yessen Aimak (Fig. 2). Although the basin was not visited, it is the locality of eight specimens donated to the author (see below). The biology of this remote lake remains poorly known.

The American Museum of Natural History Asiatic Expeditions passed the lake during a dry phase (Andrews, 1932: 301) and no description was given. The geomorphology, including geological and palaeontological data, was briefly reported by Razumowska (1946), Rozhdestvensky (1954) and Deryatkin & Liskim (1966). Subsequently, Gradzinski, Kazmierczak & Lefeld (1968) and most recently Russell & Zhai (1987) have discussed Biger Nuur. They described it as a salt lake occupying the central part of an intermontane basin between the Mongolian Altai Ridge and the granite massifs of Serkh Ula and Tayshiiven Ula. Apparently, salt marshes which periodically dry up occupy a large area around the lake.

COLLECTING LOCALITIES

Field work in Mongolia's three separate basins from the beginning of August to the end of the first week in September resulted in collections from 66 sites, designated: Net Stations (NS) 1–57, Rotenone Stations (RS) 1–7 and Fish Stations (FS) 1–2. A summary of the species and number of specimens caught is given in Table 2.

Two of these sites (FS 1–2) along the shores of Biger Nuur, Western Gobi, were not actually visited. Specimens from this lake were caught and presented to the author by Dr A. Dulma, Head of the Department of Zoology at the Institute of Biology in the Mongolian Academy of Sciences.

Net station. 1–4.

Date. 8 August 1984.

Geographical location. Main body of Tuul Gol, 5 km north of Lun, off main road after bridge west of the village, Central Aimak, MPR.

Table 2 List of species caught during 1984 survey.

	Number of specimens
Brachymystax lenok	14
Thymallus arcticus	16
Esox lucius	2
Rutilus rutilus	10
Leuciscus leuciscus baicalensis	36
Leuciscus idus	38
Leuciscus waleckii	2
Oreoleuciscus potanini 'Lake Form'	462
Oreoleuciscus potanini 'Dwarf Form'	8
Lagowskiella czekanowskii	249
Rhynchocypris steindachneri	3
Rhynchocypris costatus	3
Phoxinus phoxinus	213
Gobio gobio cynocephalus	11
Carassius auratus gibelio	34
Cyprinus carpio haematopterus	5
Noemacheilus barbatulus toni	64
Noemacheilus strauchi	80
Cobitis taenia	37
Misgurnus anguillicaudatus	41
Silurus asotus	1
Lota lota	4
Perca fluviatilis	115

Ecological notes. River about 50 m wide in broad river plain (Fig. 3) and swollen following heavy rains, with fast current over muddy bottom. Water turbid, brownish colour; temperature 22°C; conductivity 118.9μScm^{-1}.

Gear. Beach seine.

Catch: *Leuciscus idus* (27–143 mm).

Net station. 5–12.

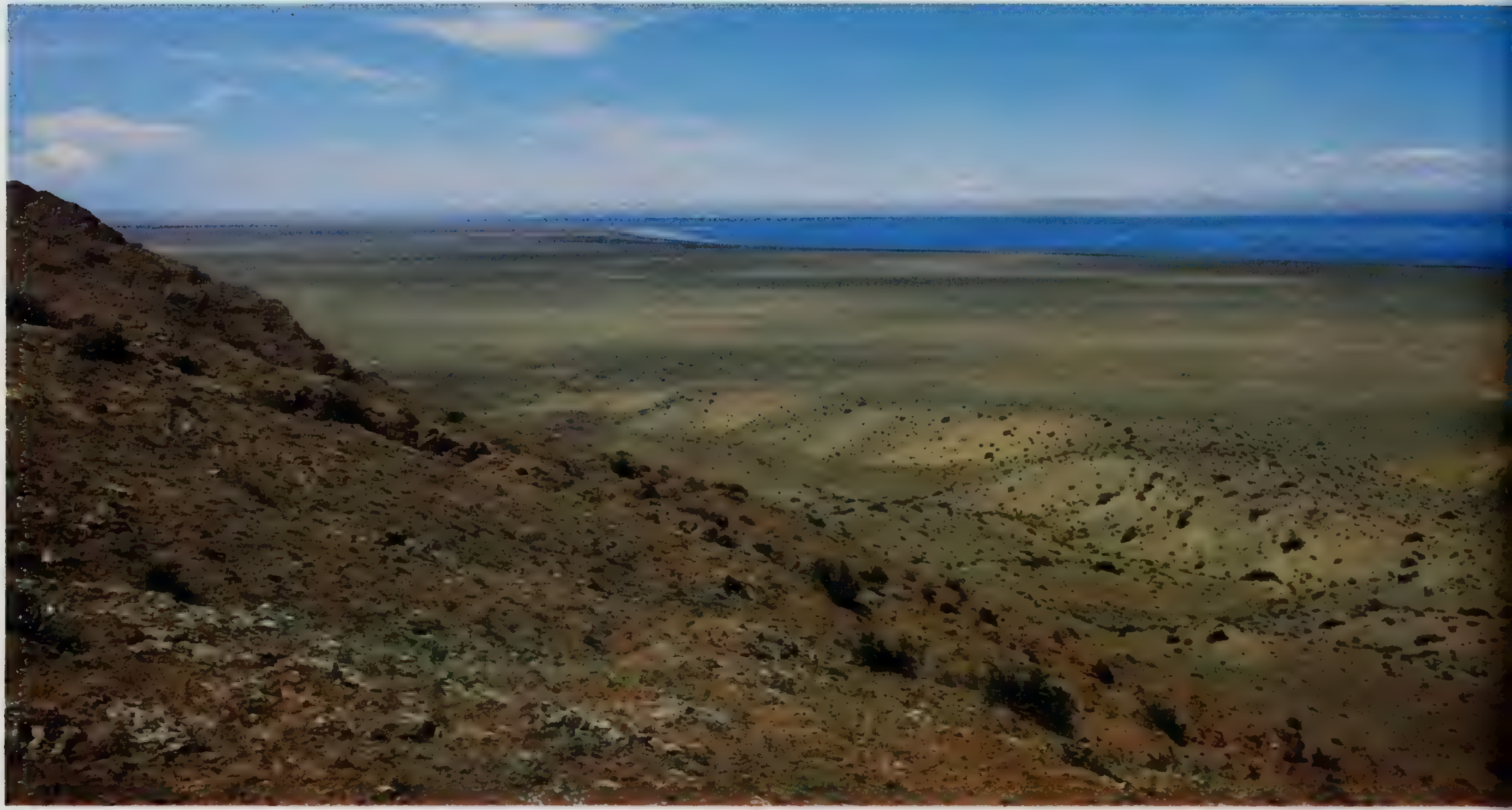
Date. 9–11 August 1984.

Geographical location. Northern shore of Ugiy Nuur, about 200 m off main track 1 km west from outlet into Orkhon Gol, Bulagan Aimak, MPR.

Ecological notes. Lake surrounded by rolling hills to the north and south, and extensive plains to the east and west. Narrow sandy-gravel, wave-washed beach, below steep grassy or eroded bank 1–2 m high (Fig. 5). Sandy-gravel substrate supports dense bank of rooted macrophytes in littoral zone extending about 20 m offshore to depth of 3 m. Clear, blue water with Secchi disc reading of 3 m above depth of 5 m; surface temperature 18.8°C; conductivity 323 and 321μScm^{-1}.

Gear. Sinking and floating gill nets set overnight for three nights, at distances between 30–200 m from shore, three beach seines from 40 m to shore (e.g. see Fig. 5) and fyke net set just beyond macrophyte bank.

Catch. Seven different species caught at this site. Gill nets yielded large *Perca fluviatilis* (222 mm & 310 mm), *Rutilus rutilus* (221–290 mm), *Leuciscus leuciscus baicalensis* (90–194 mm), *Leuciscus idus* (46–192 mm), *Esox lucius* (750 mm), *Silurus asotus* (665 mm) and *Carassius auratus gibelio* (306 mm). Each beach seine provided large numbers of juvenile *Perca* and *Leuciscus leuciscus baicalensis*. The fyke net remained empty although many medium sized *Leuciscus leuciscus baicalensis* (90–147 mm) were caught in the vertical



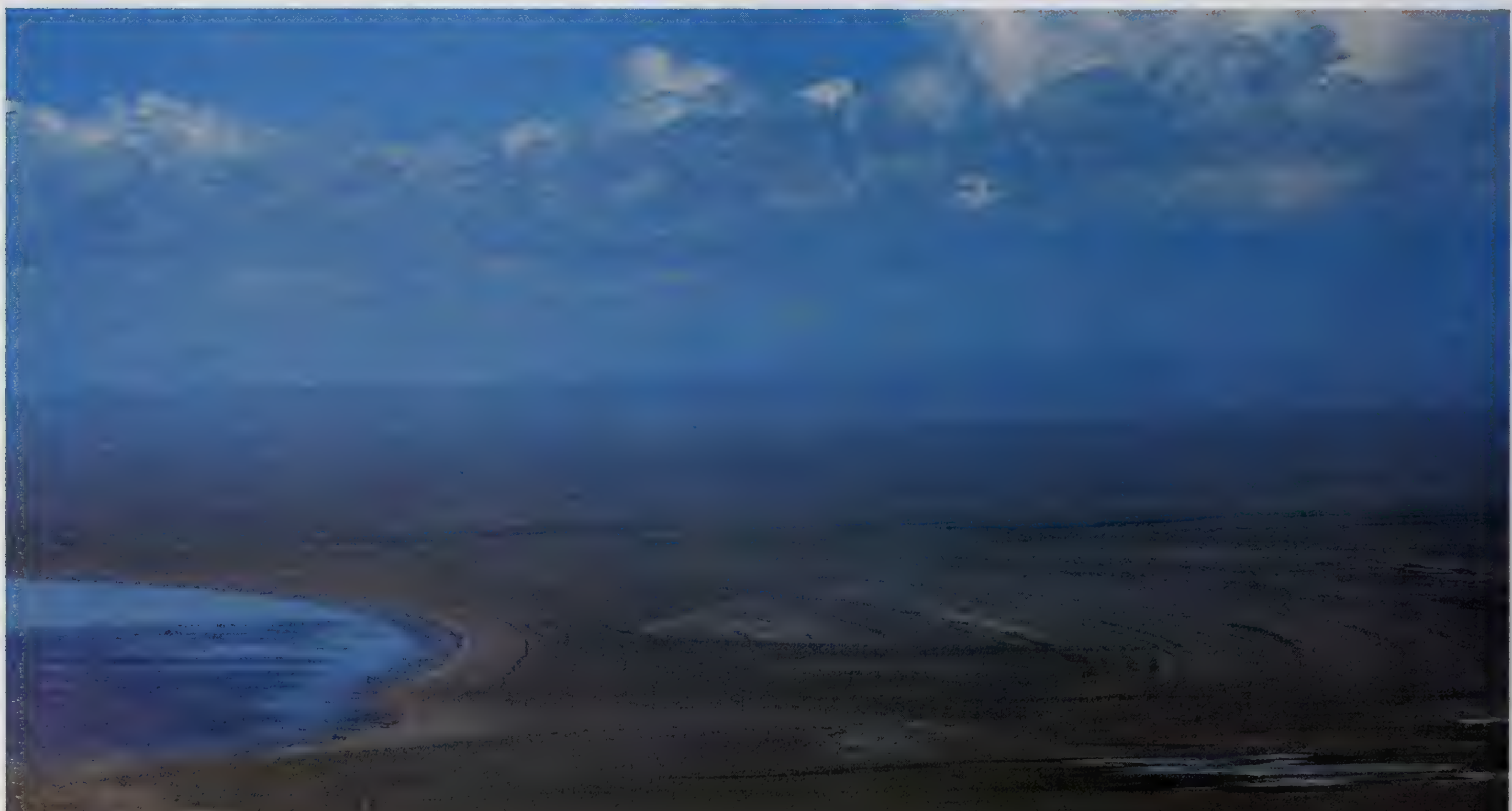
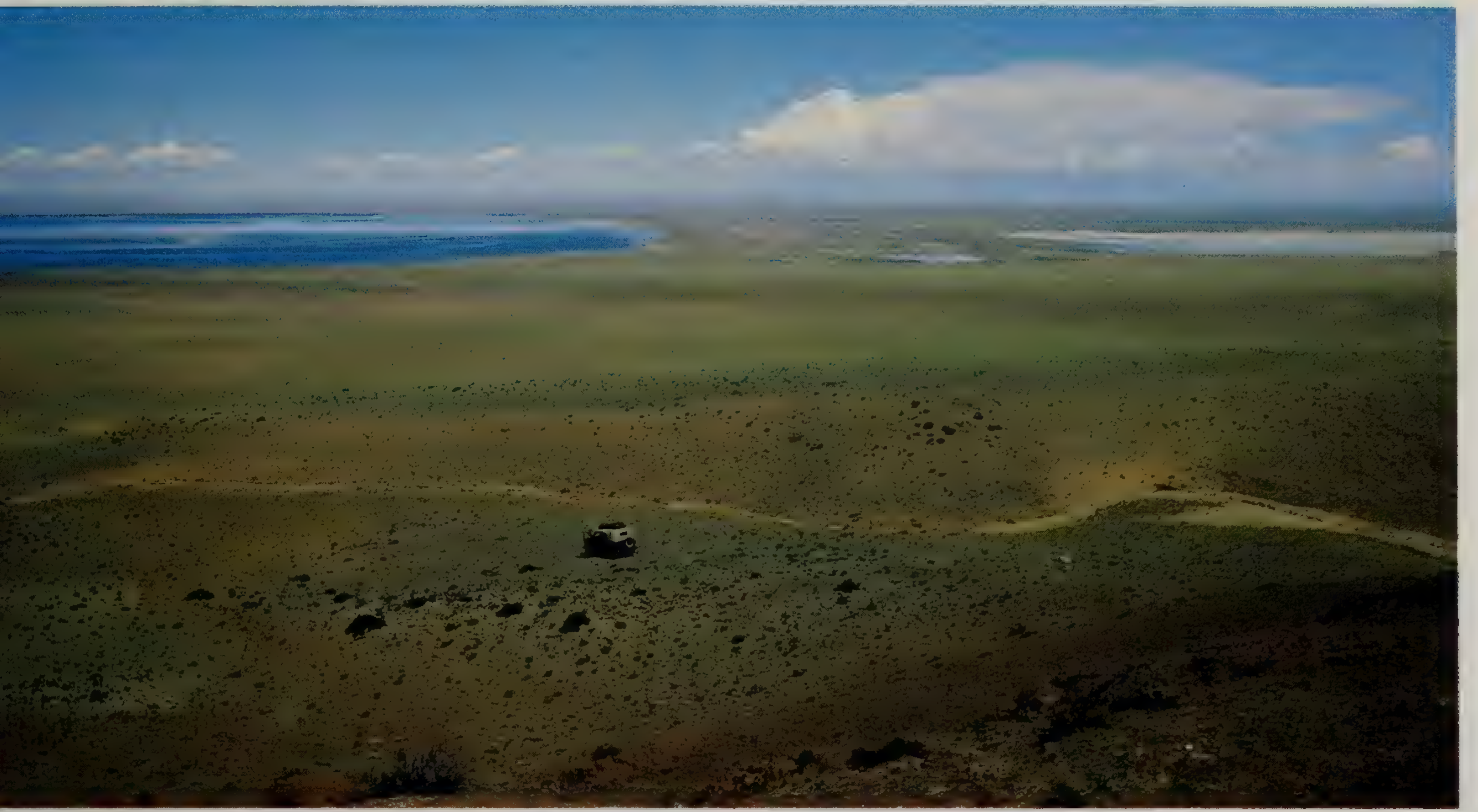
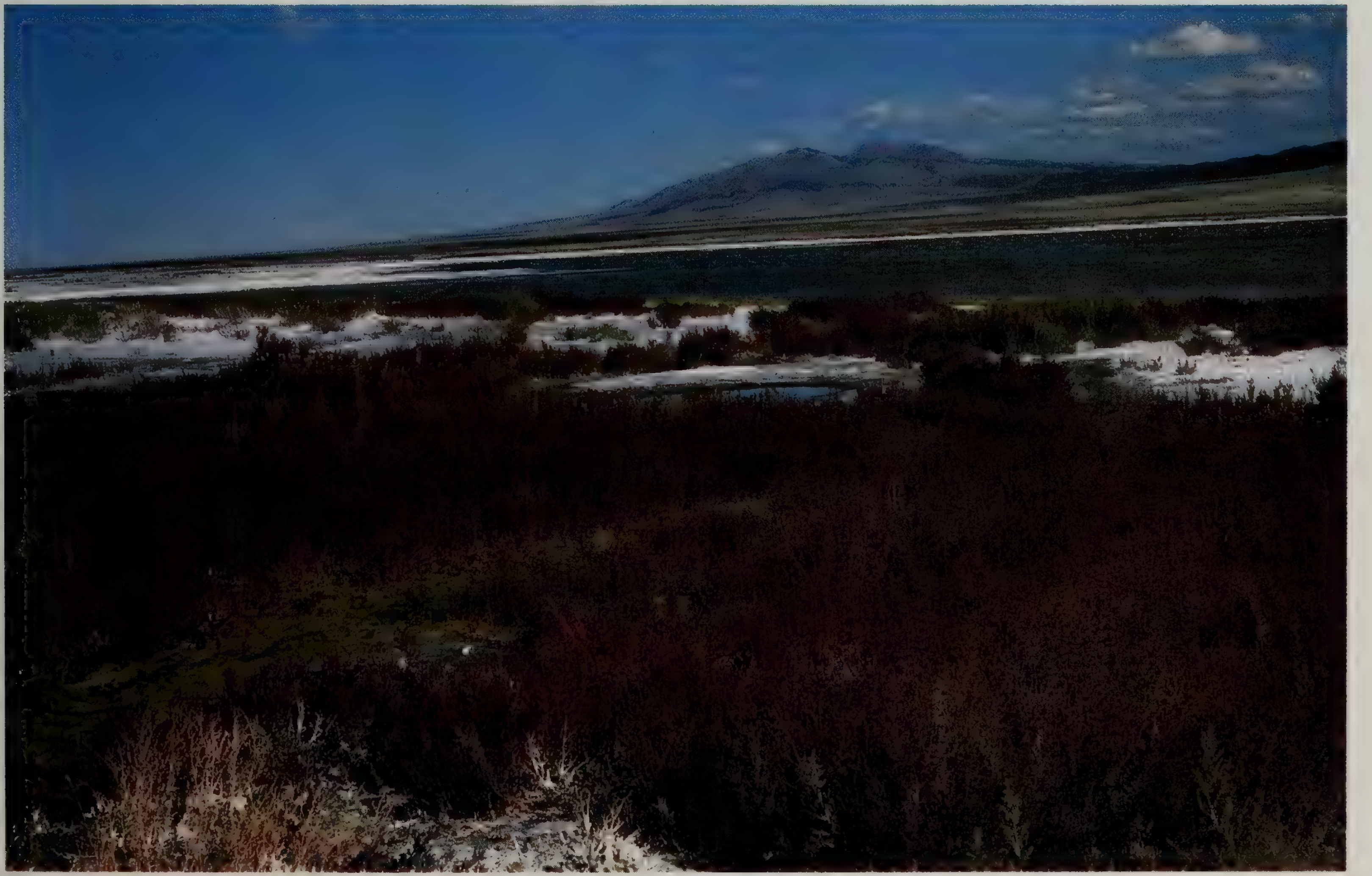


Fig. 8 Boon Tsagaan Nuur, western Gobi, Bayanhongar Aimak.
Top. Southern shore of lake viewed from above alluvial fans on foothills of Gobi Altai Mountains. East of lake, a salt pan indicates the existance of a larger water mass occuring during the recent history of the lake. A small water body is isolated between the salt pan and main body of the lake.





Bottom left. A series of relict shingle beaches appear as concentric rings along the lakes eastern shore and are evidence of its recent shrinkage; three white gurs (traditional Mongolian circular tents) can just be seen north of the lakes eastern margin and help give a scale of this vast open region of the Gobi.

Bottom right. East of the relict beaches, the small water body isolated from the main lake is surrounded by a white salty evaporate several centimetres thick and a red, salt tolerant plant (*Salicornia*).

leader net running into the mouth of the cage. Juvenile *Perca* and *Leuciscus leuciscus baicalensis* were directly observed (with the aid of mask and snorkel) feeding in the shallow littoral zone amongst the water plants (e.g. *Potamogeton* sp.).

NET STATION. 13–14.

DATE. 12 August 1984.

GEOGRAPHICAL LOCATION. Pebble shingle spit on south-eastern shore of Ugiy Nuur.

ECOLOGICAL NOTES. Spit extends for about 200 m into lake, partly subdividing eastern basin from the main body of water. Pebble and coarse gravel substrate falls away as steep gradient from spit; no macrophytes. Clear, blue water; surface temperature 16.2°C; conductivity 323μScm^{-1}.

GEAR. Gill nets set about 400 m into sub-basin overnight, and beach seine hauled off eastern and western side of pebble spit.

CATCH. Only *Perca fluviatilis* (31–244 mm), *Leuciscus leuciscus baicalensis* (29–166 mm) and *L.idus* (186 mm) were caught; adults in gill nets and juveniles in beach seine.

NET STATION. 15–17.

DATE. 13 August 1984.

GEOGRAPHICAL LOCATION. Ugiy Nuur effluent, at south-eastern margin of lake.

ECOLOGICAL NOTES. Detritus covered substrate supporting extremely dense growth of rooted macrophytes and reeds (Fig. 5). Slow current of clear water; surface temperature 17.0°C; conductivity 313μScm^{-1}.

GEAR. Gill nets set at depth of 2–5 m, 200 m offshore and in effluent channel off weedy north bank shoreline amongst submerged vegetation.

CATCH. Seven species, including *Rutilus rutilus* (188–233 mm), *Esox lucius* (head length 200 mm), *Leuciscus leuciscus baicalensis* (192 mm), *L.idus* (184 mm), *Carassius auratus gibelio* (290 mm), *Silurus asotus* (535 mm) and *Perca fluviatilis* (149 mm & 158 mm).

NET STATION. 18–19.

DATE. 15 August 1984.

GEOGRAPHICAL LOCATION. Orkhon Gol at Harhorim (Karakorum), 1 km upstream from bridge, South Khangai Aimak, MPR (Fig. 4).

ECOLOGICAL NOTES. Crystal clear, fast flowing current over substrate of well rounded pebbles in riffles and fine detritus layer supporting short aquatic weeds in pools between riffle zones; water conductivity 129μScm^{-1}.

GEAR. Beach seine hauled upstream (against current) for 40 m stretch of shallow pool between riffles, over pebble and weedy substrate; depth never exceeding half a metre. Shallow region along river bank sampled with hand-held dip net.

CATCH. Seine yielded three juvenile *Thymallus arcticus* (60–73 mm) and numerous *Phoxinus phoxinus* (16–48 mm). *P.phoxinus* was also collected by hand-net, together with numerous small loaches, including *Cobitis taenia* (49–72 mm) and *Noemacheilus barbatulus toni* (30–40 mm).

ROTENONE STATION. 1.

DATE. 15 August 1984.

GEOGRAPHICAL LOCATION. A small pool in flood plain on eastern side of Orkhon Gol, 1 km upstream from bridge at Harhorim.

ECOLOGICAL NOTES. Pool 30 m long by 5 m wide with maximum depth of just over 1 m; supplied by small stream of water from main river which returns at the pool's broadest end back into the river. Slightly turbid water over sandy, muddy substrate that supports macrophytes and dense filamentous algae.

GEAR. Rotenone applied at mouth of channel from main river and carried by current through pool before it was discharged down-stream into river.

CATCH. Within about half an hour of rotenone application, the catch consisted of juvenile *Phoxinus phoxinus* (12–54 mm), *Noemacheilus barbatulus toni* (25–56 mm) and *Cobitis taenia* (20–58 mm).

NET STATION. 20–21.

DATE. 16 August 1984.

GEOGRAPHICAL LOCATION. Hogshin Orkhon Gol, a high gradient head-water of Orkhon Gol, about 60 km south from Harhorim along mountainous pass to Arvayheer, South Khangai Aimak, MPR.

ECOLOGICAL NOTES. At the first station the stream courses across a high altitude alpine meadow and is about 1.5 m wide and 0.5 m deep, with a swift current of brown turbid water over a muddy substrate; slightly high river level was a result of recent rainstorm. The second station was close to the source of the river, at the head of the valley, and was made before starting the descent to Arvayheer. Here the stream is a few centimetres deep, about 0.5 m wide and runs over a substrate of coarse gravel and mud.

GEAR. Hand-held net.

CATCH. From the first station, consisted of *Cobitis taenia* (56 mm) and several *Noemacheilus barbatulus toni* (34–90 mm). The second station yielded only *N.barbatulus toni* (47–105 mm).

NET STATION. 22.

DATE. 17 August 1984.

GEOGRAPHICAL LOCATION. Spring fed freshwater stream meandering across water meadow about 40 m from eastern shore of Boon Tsagaan Nuur in valley of western Gobi, Bayanhongar Aimak, MPR.

ECOLOGICAL NOTES. Slight current of pure, clear water several centimetres deep, above sandy/muddy substrate supporting a variety of aquatic plants.

GEAR. Hand-held net.

CATCH. Juvenile *Oreoleuciscus potanini* (16–38 mm)

NET STATION. 23–26.

DATE. 18 August 1984.

GEOGRAPHICAL LOCATION. Boon Tsagaan Nuur, an endorheic deflation lake about 45 km long by 20 km wide, in western Gobi Valley (Fig. 7).

ECOLOGICAL NOTES. Eastern shore of lake consists of typical low gradient sandy beach, no macrophyte growth. Water somewhat turbid due to prominent algal bloom and aggregated algal masses. Water temperature 17.2°C; Secchi disc reading 0.8 m at a depth of 2.2 m, 200 m off eastern shore; water conductivity 5892μScm^{-1}.

GEAR. Fleet of sinking and floating gill nets (mesh size 2–10 cm) employed over-night, 200 m offshore at depth of 2 m.

CATCH. Numerous *Oreoleuciscus potanini* ('Lake Form') only. Smallest mesh net (2 cm i.e. NS 23) caught fishes in size range between 89–150 mm; many between 100–150 mm SL were in a reproductively active state and readily shed gametes when handled. Medium mesh net (6 cm i.e. NS 24) caught fishes in size range between 150–300 mm SL, many shedding milt or spawn. Similar net set in lake opposite mouth of inflowing river, at depth of 1.1 m yielded a lighter catch of generally larger individuals (i.e. NS 25; 269–327 mm SL). Net with largest mesh size (10 cm) positioned opposite river mouth, yielded nothing.

NET STATION. 27–28.

DATE. 19 August 1984.

GEOGRAPHICAL LOCATION. Boon Tsagaan Nuur, 1–1.5 km off eastern shore.

ECOLOGICAL NOTES. Water temperature 21.2°C; conductivity 6160μScm^{-1} and 6379μScm^{-1} above depths of 4.5 m and 2.4 m respectively; Secchi disc 1.2m at both depths.

GEAR. Sinking gill nets, 6 & 10 cm mesh size, employed at depths of 4.5 m (NS 27) and 4.1 m (NS 28).

CATCH. Numerous *Oreoleuciscus potanini* (150–348 mm), many spawning, yielded by former (NS 27); the latter (NS 28) produced nothing.

NET STATION. 29–30.

DATE. 20 August 1984.

GEOGRAPHICAL LOCATION. Boon Tsagaan Nuur about 2 km off eastern shore.

ECOLOGICAL NOTES. Water temperature 21.6°C; conductivity 6270μScm^{-1}; Secchi disc 1.1 m above a total depth of 9.75m.

GEAR. Combined sinking and floating 6 cm mesh size gill nets.

CATCH. Heavy overnight storm, followed by violent winds which lasted for three days, made net retrieval impossible. After storm had dissipated, nets could not be located; water temperature 14.8°C and conductivity 5506μScm^{-1}.

NET STATION. 31.

DATE. 21 August 1984.

GEOGRAPHICAL LOCATION. Tsagaan Gol, tributary of Baydarag Gol, Western Gobi (Bayanhongar Aimak); about half a kilometre from mouth on north eastern shore of Boon Tsagaan Nuur (Fig. 7).

ECOLOGICAL NOTES. Crystal clear swift current of fresh water 20 m wide with maximum depth of 1 m over a substrate of fine gravel with no sign of macrophytes; conducticity 244μScm^{-1}.

GEAR. Gill net, 4cm mesh size, strung between banks overnight.

CATCH. Nothing.

ROTENONE STATION. 2.

DATE. 22 August 1984.

GEOGRAPHICAL LOCATION. Small tributary of Tsagaan Gol, supplied by spring emanating from meadow bordering Boon Tsagaan Nuur.

ECOLOGICAL NOTES. Crystal clear current of fresh water over a substrate of fine gravel. 1–4 m wide with a maximum depth of half a metre; conductivity 193μScm^{-1}.

GEAR. Rotenone applied to small blind inlet of tributary with slow moving current and some algae and small rooted aquatic plants.

CATCH. Large numbers of juvenile *Oreoleuciscus potanini* (10–86 mm) and two juvenile *Noemacheilus strauchi* (30 & 26 mm).

ROTENONE STATION. 3.

DATE. 22 August 1984.

GEOGRAPHICAL LOCATION. Small isolated pool in river channel on eastern side of main course of Tsagaan Gol, about half kilometre from mouth into Boon Tsagaan Nuur. (Fig. 7).

ECOLOGICAL NOTES. Still, murky water supporting algae and some small rooted aquatic plants.

GEAR. Rotenone applied at several points along pool.

CATCH. Numerous juvenile *Oreoleuciscus potanini* (10–37 mm).

ROTENONE STATION. 4.

DATE. 22 August 1984.

GEOGRAPHICAL LOCATION. Narrow channel on western side of Tsagaan Gol, about half kilometre from its mouth into Boon Tsagaan Nuur.

ECOLOGICAL NOTES. Channel 30 m long, 6 m wide, with maximum depth of 2 m. Closed at north end with freshwater emanating from spring and passing along channel to southern end and open connection with Tsagaan Gol. Murky water supports algae and other aquatic plants.

GEAR. Rotenone applied to north end of channel and carried by current to its mouth.

CATCH. Numerous juvenile *Oreoleuciscus potanini* (10–40 mm) and *Noemacheilus strauchi* (39–66 mm).

ROTENONE STATION. 5.

DATE. 26 August 1984.

GEOGRAPHICAL LOCATION. Pool in water meadow off north bank of Tamir Gol, 2–3 km upstream from confluence with upper reaches of Orkhon Gol, adjacent to Ugiy Nuur, North Khangai Aimak, MPR.

ECOLOGICAL NOTES. Crystal clear water to about 1 m depth in 6 m wide pool containing dense aquatic plants (e.g. *Potamogeton* sp.).

GEAR. Rotenone.

CATCH. Nothing.

NET STATION. 32–36.

DATE. 26 August 1984.

GEOGRAPHICAL LOCATION. North bank of Tamir Gol, 2–3km upstream from confluence with upper reaches of Orkhon Gol, adjacent to Ugiy Nuur.

ECOLOGICAL NOTES. River in spate following heavy rains, extremely swift, strong current of brown turbid water (Fig. 3). Numerous small streams course across quite densely vegetated bank to supply small pools in wide flood plain; willow stands common along bank.

GEAR. Seine net dredged against current along stretch of stream in flood plain and hand-held dip net dragged through water along bank of main river and small inflowing stream.

CATCH. *Brachymystax lenok* (106 & 165 mm), *Thymallus arcticus* (51–74 mm), *Leuciscus leuciscus baicalensis* (162 mm), *Phoxinus phoxinus* (2–54 mm), *Noemacheilus barbatulus toni* (30–62 mm) and *Cobitis taenia* (53–73 mm).

NET STATION. 37–40.

DATE. 29–30 August 1984.

GEOGRAPHICAL LOCATION. Inlet along west bank of Terilg Gol, at end of vehicle track just east of recreation centre 35 km east of Ulan Bator, Central Aimak, MPR (Fig. 4).

ECOLOGICAL NOTES. High gradient riffles of fast clear water over pebble and rock substrate. Inlet separated from main river by pebble bar lined with willow shoots; main river bank generally low and tree lined, with young pine and birch. Inlet channel 35 m long, 8 m wide and not more than 1.5 m deep, contained murky water and some aquatic plants.

GEAR. Four night hauls up channel with seine, letting it extend into main river before hauling to blind end of inlet. Gill net (4 cm mesh) suspended between pebble bar and bank overnight.

CATCH. *Brachymystax lenok* (53–408 mm), *Thymallus arcticus* (148–251 mm), *Leuciscus leuciscus baicalensis* (260 mm), *Noemacheilus barbatulus toni* (100 m) and *Lota lota* (376 mm).

NET STATION. 41–42.

DATE. 31 August 1984.

GEOGRAPHICAL LOCATION. Terilg Gol inlet and pool at end of vehicle track beyond recreation centre, 35 km east of Ulan Bator.

ECOLOGICAL NOTES. Pool was 3–4 m deep with slow current of murky water over submerged vegetation which was particularly dense in sheltered region below a 20 m high rocky embankment covered in young willow and birch saplings.

GEAR. Sinking gill nets (4 cm) set overnight across inlet and pool.

CATCH. Nothing caught from inlet, water level had dropped since arrival at this locality and channel quite shallow compared to two previous nights. Catch from pool consisted of *Thymallus arcticus* (183–219 mm) and *Lota lota* (257–289 mm).

NET STATION. 43

DATE. 1 September 1984.

GEOGRAPHICAL LOCATION. Stream meandering across flood plain off western bank of Herelen Gol, about 60 km downstream from main bridge in Kentei Aimak, MPR.

ECOLOGICAL NOTES. Stream about 12 m wide and depth not exceeding 2 m, had a moderate current of murky water over a muddy substrate.

GEAR. Hand-held net.

CATCH. *Lagowskiella czekanowskii* (16–48 mm), *Rhynchocypris costatus* juvenile (43 mm), *Phoxinus phoxinus* (21 & 50 mm), *Gobio gobio cynocephalus* (21 & 22 mm), *Cobitis taenia* (52–79 mm) and *Misgurnus anguillicaudatus* (20–81 mm).

NET STATION. 44–45.

DATE. 1 September 1984.

GEOGRAPHICAL LOCATION. West bank of Herelen Gol, about 60 km downstream of the main bridge, Kentei Aimak.

ECOLOGICAL NOTES. At this point, river runs beneath a high eastern escarpment face (Fig. 6) and has a width of 50–100 m as it cuts through a terraced flood plain of 2–3 km in width. Rich variety of flowering plants cover the flood plain and attract butterflies and other flying insects. River in spate following heavy rains, bank not clearly visible (Fig. 6).

GEAR. Beach seine hauled across two flooded water meadows adjacent to main, fast flowing river.

CATCH. *Leuciscus leuciscus baicalensis* (190 mm; cf *brevirostris* Mori, 1938).

NET STATION. 46–47.

DATE. 1 September 1984.

GEOGRAPHICAL LOCATION. Main stream of Herelen Gol, west bank, 60 km downstream from bridge, Kentei Aimak.

ECOLOGICAL NOTES. Powerful current of brown turbid water over a muddy substrate; region fished sheltered from main force of current by willow stand (Fig. 6).

GEAR. Seine net dropped from dinghy 20 m off bank.

CATCH. Nothing.

NET STATION. 48–49.

DATE. 2 September 1984.

GEOGRAPHICAL LOCATION. Side channel off west bank of Herelen Gol, 60 km downstream from bridge, Kentei Aimak.

ECOLOGICAL NOTES. Channel divided from main river by pebble and mud bank supporting Willow shoots. Swift current of brown, murky water not with force found in main stream and decreasing in strength from previous day.

GEAR. Sinking gill nets (2 & 4 cm mesh) secured to willow shoot and allowed to be taken with current, left overnight.

CATCH. *Brachymystax lenok* (196–315 mm).

NET STATION. 50.

DATE. 2 September 1984.

GEOGRAPHICAL LOCATION. Rivulet half a kilometre east of western bank of Herelen Gol, 60 km downstream from bridge, Kentei Aimak.

ECOLOGICAL NOTES. Slow current of clear water, 10–20 m wide and several metres deep above a muddy substrate supporting dense growth of aquatic plants. Rivulet expands into pool along its course, macrophytes and reeds numerous.

GEAR. Seine hauled across pool in evening.

CATCH. Nothing; this could have been partly due to vegetation hindering net.

NET STATION. 51–53.

DATE. 3 September 1984.

GEOGRAPHICAL LOCATION. Side channel and main stream of Herelen Gol, 60 km downstream from bridge, Kentei Aimak.

ECOLOGICAL NOTES. Brown, turbid water continuing to drop in level compared to previous days; current in main stream still powerful.

GEAR. Sinking gill nets (2 & 4 cm mesh) set in 1–2 m of water, secured to willow stands and left overnight.

CATCH. Net in main stream (i.e. NS 51) empty, those in side channel caught *Brachymystax lenok* (400 mm), *Rhynchocypris steindachneri* (110 mm), *Rhynchocypris costatus* (160 mm) and two juvenile *Carassius auratus gibelio* (89 & 91 mm).

NET STATION. 54–56.

DATE. 4 September 1984.

GEOGRAPHICAL LOCATION. Side channel off main stream of Herelen Gol, 60 km downstream from road bridge, Kentei Aimak.

ECOLOGICAL NOTES. Brown, turbid water with relatively swift current; water level lower than at previous days.

GEAR. Hand-held net hauled along shallow water off west bank and sinking gill nets (2 & 4 cm mesh) secured to willow stands and left to drift into main stream by powerful current (Fig. 6).

CATCH. *Rhynchocypris steindachneri* (136 mm), *Phoxinus phoxinus* (37–43 mm), *Gobio gobio cynocephalus* (110 mm), *Carassius auratus gibelio* (90 mm), *Noemacheilus barbatulus toni* (juvenile, 29 mm), *Cobitis taenia* (60 mm) and *Lota lota* (180mm).

NET STATION. 57.

DATE. 4–5 September 1984.

GEOGRAPHICAL LOCATION. Pool along rivulet in water meadow about half a kilometre from main stream Herelen Gol, 60 km down-stream from bridge, Kentei Aimak.

ECOLOGICAL NOTES. Pool supports dense growth of macrophytes and reeds.

GEAR. Sinking gill net (3 cm mesh) left for two consecutive nights.

CATCH. *Rutilus rutilus* (371 mm), *Rhynchocypris steindachneri* (115 mm) and several juvenile *Carassius auratus gibelio* (87–95 mm).

ROTENONE STATION. 6.

DATE. 5 September 1984.

GEOGRAPHICAL LOCATION. Pool along rivulet in water meadow described for NS 50 & 57.

ECOLOGICAL NOTES. Eastern region of deep, permanent pool of clear water with slow current over dense aquatic vegetation (see NS 50 & 57 above).

GEAR. Rotenone.

CATCH. Nothing apart from some water snails.

ROTENONE STATION. 7.

DATE. 5 September 1984.

GEOGRAPHICAL LOCATION. Isolated pond in water meadow, about half a kilometre from west bank of Herelen Gol and close to rivulet (NS 50 & 57) draining flood plain.

ECOLOGICAL NOTES. At times of high water, pond may temporarily be joined to rivulet (Fig. 6). Pond appears to be permanent and supports partly submerged reeds around its perimeter and dense growth of fully submerged rooted macrophytes which were clearly observed through the clear water.

GEAR. Rotenone applied evenly around pond.

CATCH. *Lagowskiella czekanowskii* (20–60 mm), *Rhynchocypris costatus* (40 mm), *Phoxinus phoxinus* (36 mm), *Gobio gobio cynocephalus* (20–60 mm), *Carassius auratus gibelio* (30–55 mm) and *Misgurnus anguillicaudatus* (36 mm).

SYSTEMATIC ACCOUNT

This account deals only with the specimens obtained during the 1984 ichthyological survey in the Mongolian People's Republic.

Twenty-two species of primary freshwater fishes, representing eight families, are detailed in systematic order. The specimens have been incorporated into the collections of the British Museum (Natural History); abbreviated as BM(NH). Net or rotenone station, register number and standard length are given for all specimens.

Initial identifications were made using standard works on the fishes of the USSR (Berg, 1948), Mongolian People's Republic (Shatunovskii, 1983 & 1985) and People's Republic of China (Nichols, 1943). Many taxonomic problems associated with the fishes from these regions were revealed which required reference to specialist literature. Where a taxon has been recently revised by a specialist of the group (e.g. Holčík & Skořepa, 1971 for *Rutilus*, or Howes, 1985 for *Phoxinus*), attention was given to their taxonomic proposals.

Where necessary, the specialist literature was supplemented by comparison with type and other material held at the BMNH and Museum National d'Histoire Naturelle, Paris (MNHN) or obtained on loan from the American Museum of Natural History (AMNH). Intraspecific variation, geographical range, ecological notes and a taxonomic discussion are given for each species.

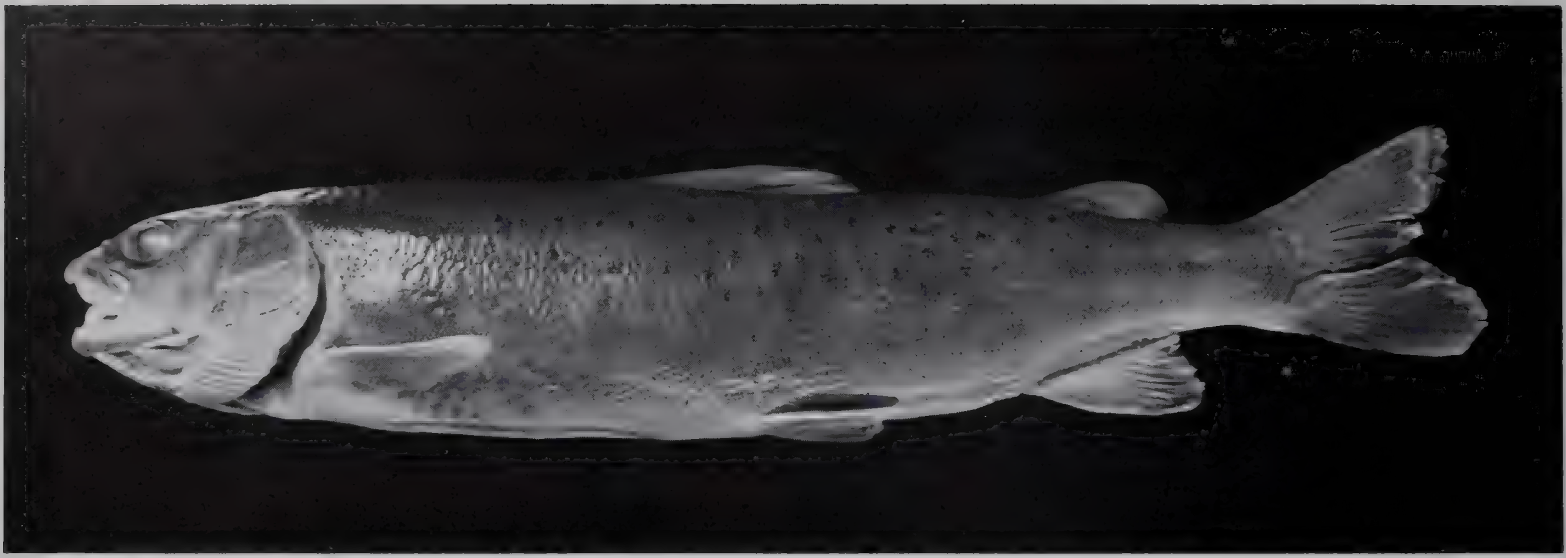


Fig. 9 *Brachymystax lenok* in lateral view (237 mm SL; BMNH 1986.8.28: 3–5).

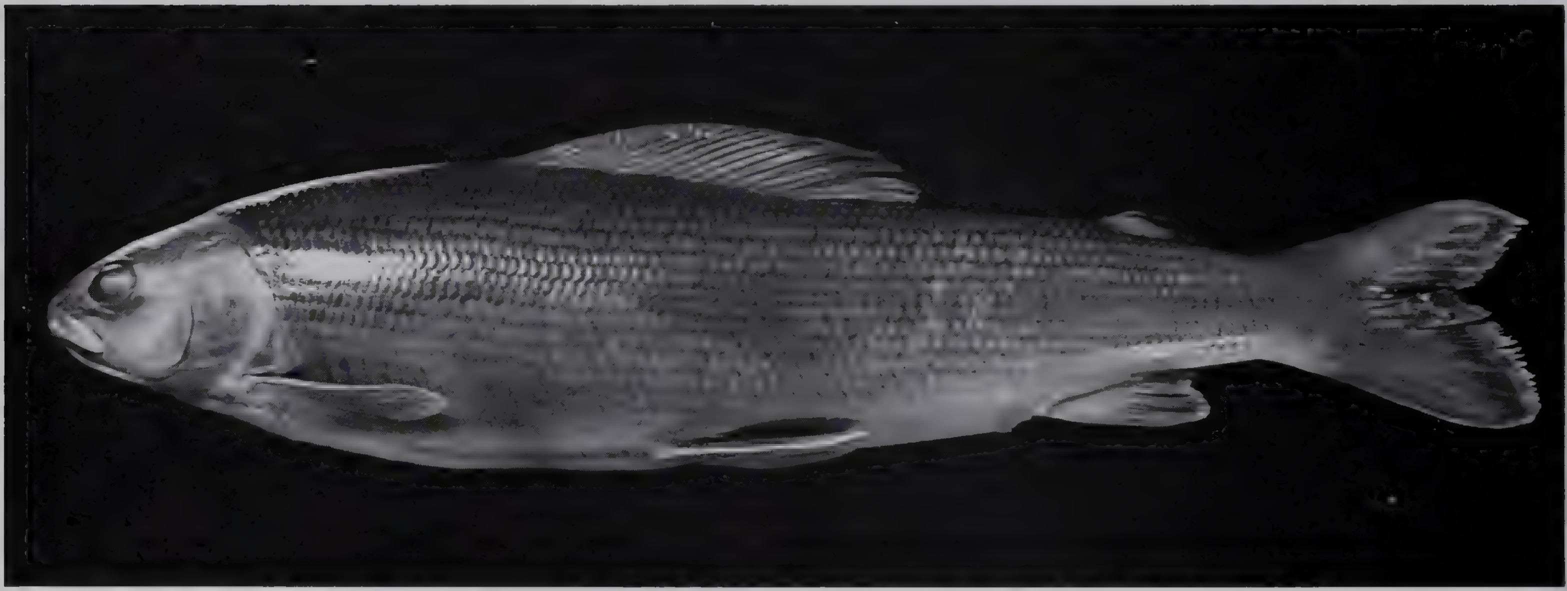


Fig. 10 *Thymallus arcticus*, lateral view (165 mm SL; BMNH 1986.8.28: 27–28)

SALMONIDAE

SALMONINAE

Brachymystax lenok **(Pallas, 1773)**

Fig. 9

MATERIAL. NS 36, 1986.8.28: 1–2 (106 & 165 mm); NS 37, 1986.8.28: 3–5 (226–237 mm); NS 37, 1986.8.28: 6 (408 mm)) NS 38, 1986.8.28: 7–8 (236–247 mm); NS 40, 1986.8.28: 9 (53 mm); NS 48, 1986.8.28: 10–11 (236 & 315 mm); NS 49, 1986.8.28: 12–13 (196 & 248 mm); NS 52, 1986.8.28: 14 (400 mm). Total 14 specimens.

VARIATION. Morphometric diagnosis of this monotypic genus given by Berg (1948), Holčík & Pivnička (1968: 4) and Shatunovskii (1983 & 1985 see figs. 2 & 3). A prominently pink coloured ventral region present in my specimens was not mentioned in Berg's colour description (1948: 320); maybe it is coloration associated with the breeding cycle.

GEOGRAPHICAL RANGE. Extends from the Ob River in western Siberia, east to the Amur River and its tributaries in the USSR and North China.

ECOLOGICAL NOTES. In Mongolia collected from the main stream and side channels of the Terilg Gol (Arctic basin) and Herelen Gol (Pacific basin); a distribution that supports that proposed by Shatunovskii (1983: 114).

TAXONOMIC DISCUSSION. A *Brachymystax* species was reported by Mori (1938 and see Berg, 1948: 318) from the Upper Yalu River. I suspect this species in which '... the snout is strongly elongated forming a fleshy cone projecting forward above the lower jaw' (Berg, 1948: 318) is a *Rhynchocypris* (sensu Howes, 1985; see below p. 197) and is not referrable to *Brachymystax lenok*.

The Upper Yalu River forms the natural border between North Korea and China (PRC) and may, historically, or even seasonally, be connected with the Amur River system by southern tributaries of the Sungari River. *Brachymystax* was caught together with *Rhynchocypris* during the course of this survey in the Herelen Gol, a Mongolian headwater of the Amur River.

THYMALLINAE

Thymallus arcticus **(Pallas, 1776)**

Fig. 10

MATERIAL. NS 19, 1986.8.28: 15–17 (60–73 mm); NS 32, 1986.8.28: 18–21 (51–74 mm); NS 37, 1986.8.28: 22–26 (148–

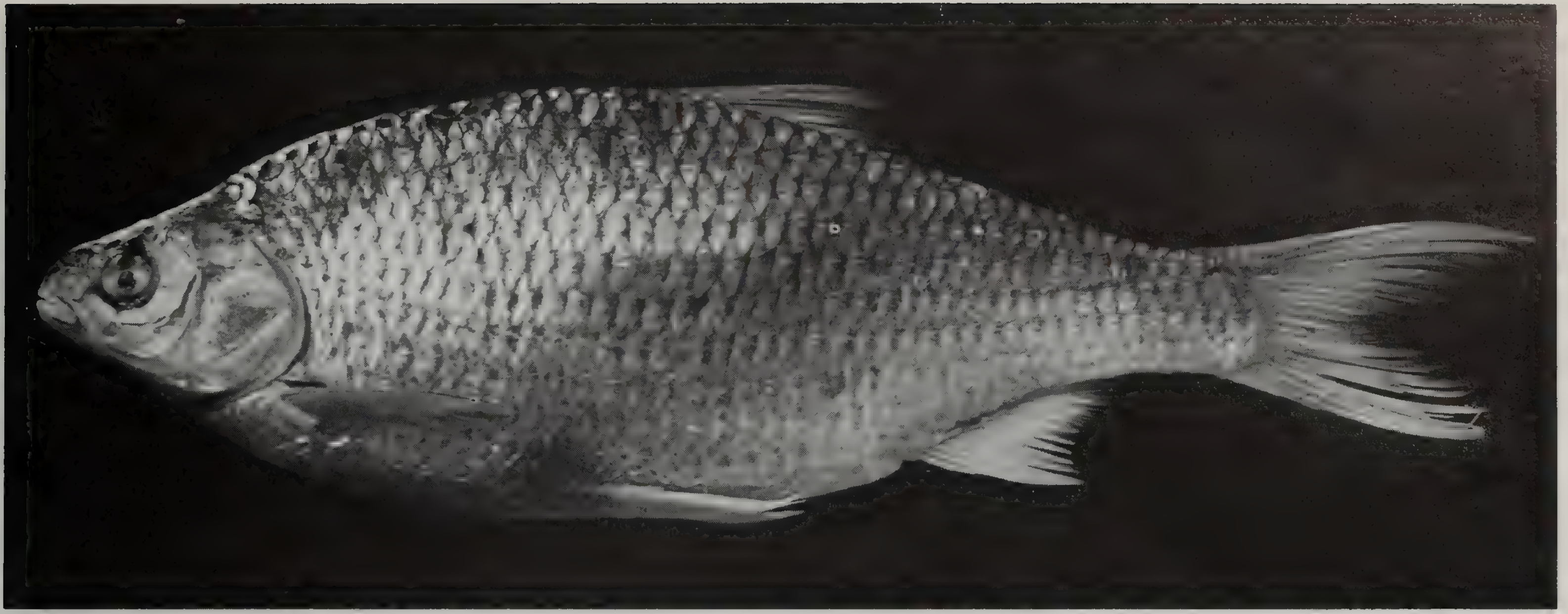


Fig. 11 *Rutilus rutilus*, lateral view (271 mm SL; BMNH 1986.8.28: 33–35).

251 mm); NS 38, 1986.8.28: 27–28 (165–192 mm); NS 41, 1986.8.28: 29–30 (183–219 mm). Total 16 specimens.

VARIATION. Agree with description given by Berg (1948: 449), Holčík & Pivnička (1968: 4) and Shatunovskii (1983: 127 and 1985: 56).

GEOGRAPHICAL RANGE. Has a holarctic distribution (Scott & Crossman, 1973) which extends south in Asia to northern Mongolia and the Upper Yalu River.

ECOLOGICAL NOTES. Within Mongolia is confined to waters of the Arctic basin and was caught in the main stream and inlets of the Orkhon, Tamir and Terilg Gols.

TAXONOMIC DISCUSSION. Distinct subspecies are recognised in other regions of Mongolia including, in Pacific draining headwaters of the Amur River system, the subspecies *Thymallus arcticus grubei* (Berg, 1948; Shatunovskii, 1983) and, in Khobsogul Nuur, the lacustrine subspecies *Thymallus arcticus nigrescens* (Scott & Crossman, 1973). In addition to these, attention should be given to a single specimen described by Boulenger (1898) as *Phylogephyra altaica*, a monotypic genus '. . . from the south side of the Altai Mountains . . . brought home by Mr St. George Littledale'.

Boulenger (1898) believed this species '. . . completely bridges over the gap' between the two groups designated at that time as Salmoninae and Coregoninae and '. . . approaches the genus *Thymallus*'; in particular *T.brevirostris*. Berg (1909) synonymised *P.altaica* with *T.brevirostris* and most subsequent authors have followed his decision (e.g. Svetovidov, 1936; Shatunovskii, 1983 & 1985), even though *T.brevirostris* is confined to the western Mongolian Great Lakes basin while the type locality of *altaica* lies outside this enclosed system.

As part of a systematic study of the Salmonidae, Benke (1965: 234) examined the holotype of *Phylogephyra altaica* and concluded the genus should be retained. I support his view that *altaica* represents a distinct thymalline species. Although the type is in a poor state, it represents a taxon quite distinct from other *Thymallus* species in several characters (e.g. head length; jaw cleft position posterior to eye; large, strong caniniform teeth on jaws, vomer and palatines; 12 pelvic fin rays; only 7–8 scales dorsal to the lateral line).

Whether these differences merit *altaica* being placed in a distinct genus (i.e. *Phylogephyra*, as proposed by Boulenger, 1898) must await a further analysis of thymalline interspecific relationships. For the present, *altaica* must be removed from the synonymy *T.brevirostris*, be recognised as a distinct species of *Thymallus* and be considered as an additional member of the Mongolian fish fauna.

ESOCIDAE

Esox lucius Linnaeus, 1758

MATERIAL. NS 9, 1986.8.28: 31 (246 mm head length, to posterior edge of operculum); NS 16, 1986.8.28: 32 (200 mm head length, to posterior edge of operculum). Total 2 specimens (both incomplete; head with pectoral girdle attached and caudal fin).

VARIATION. Agree with the diagnosis given by Berg (1948) and Shatunovskii (1983: 133) who based his description on 50 specimens from the same lake (Ugiy Nuur).

GEOGRAPHICAL RANGE. Widespread across freshwaters of Eurasia from the British Isles and western Europe to the headwaters of Arctic draining systems of eastern USSR.

ECOLOGICAL NOTES. This is the only species of pike present in Mongolian Arctic basin waters and was caught during this survey in Ugiy Nuur. In both cases the fishes appeared to be attracted to gill nets of small mesh size (i.e. 2 & 3 cm) by the presence of suitable prey (e.g. *Leuciscus idus*) caught in the nets. In an attempt to engulf prey, *E.lucius* became caught by twine looped around its large caniniform teeth.

TAXONOMIC DISCUSSION. A second species, *Esox reicherti*, is endemic to the Amur basin (Shatunovskii, 1983; Scott & Crossman, 1973: 357) and is considered to be part of the Mongolian fauna. However, it was not caught from localities sampled during the course of this survey.

CYPRINIDAE

Rutilus rutilus (Linnaeus, 1758)

Fig. 11

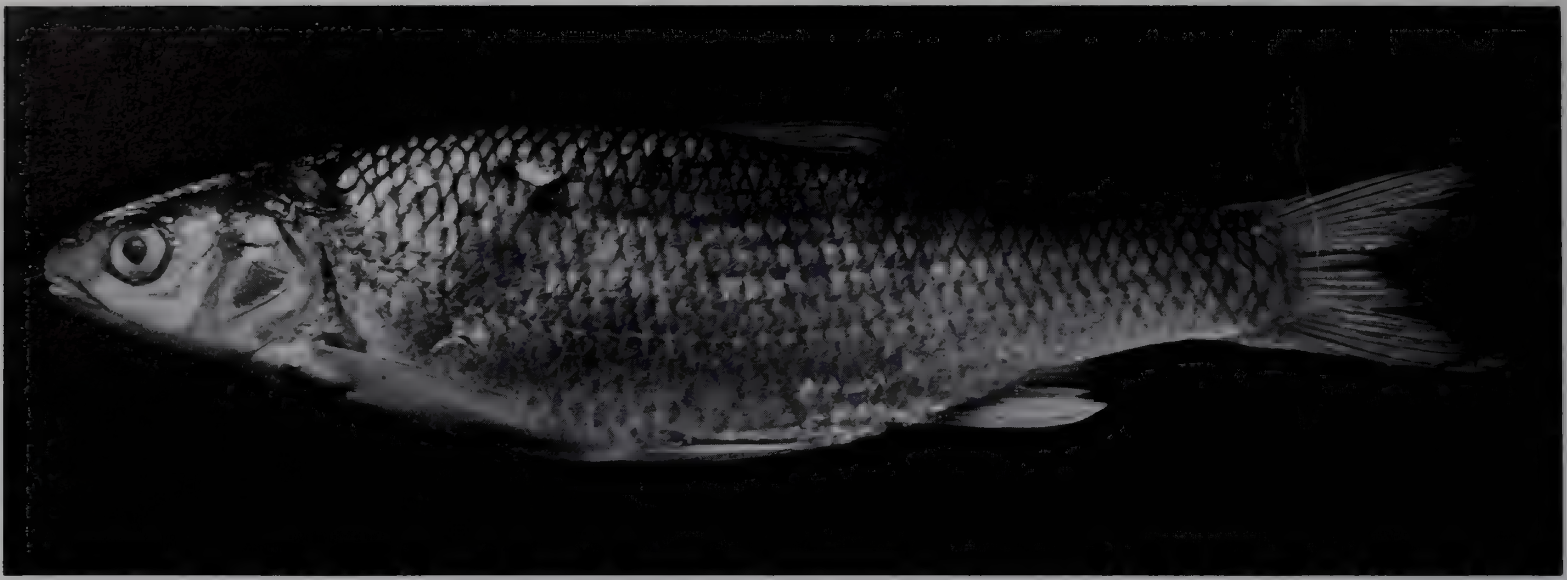


Fig. 12 *Leuciscus leuciscus baicalensis*, lateral view (192 mm SL: BMNH 1986.8.28: 77).

Material. NS 5 & 6, 1986.8.28: 33–35 (271–290 mm); NS 9, 1986.8.28: 36 (221 mm); NS 10 & 11, 1986.8.28: 37–40 (230–243 mm); NS 16, 1986.8.28: 41–42 (188–223 mm). Total 11 specimens.

Variation. Agree with the diagnosis given by Berg (1948: 499) and more recently by Shatunovskii (1983: 40) for the subspecies *R.rutilus lacustris*.

Geographical range. Has a typical Eurasian distribution extending from England in the west to the Lena River in the east, and from the Ob River in the north to the watershed of the Caspian and Aral seas in the south.

Ecological notes. Within Mongolia *R.rutilus* is confined to Arctic draining waters and was caught in abundance in Ugiy Nuur. It is not surprising, therefore, that these specimens coincide closely with the diagnosis given by Shatunovskii (1983) as it was based on 31 specimens from the same lake. The length of the largest specimen caught during this survey (290 mm) exceeds that recorded by Berg (1948), Holčík & Skořepa (1971) or Shatunovskii (1983).

The diet of *R.rutilus* is varied (Wheeler, 1969: 207) and consists as much of plant material (e.g. diatoms, filamentous algae and macrophytes) as animal foods (e.g. planktonic larvae, insects, freshwater shrimps, aquatic isopods and molluscs). Analysis of gut contents of Ugiy Nuur specimens revealed, in general, remains of plant, insect and mollusc material.

Taxonomic discussion. The degree of overlap between meristic and morphometric subspecific characters described by Berg (1948) indicates the possibility of clinal variation. Holčík and Skořepa (1971) revised the taxonomy of the species, using comparative series of specimens from populations covering the whole area of distribution. They concluded that '... *Rutilus rutilus* exhibits only relatively minor variation in morphological features' to the extent that it '... has not yet evolved such distinct morphological and biological populations that the term subspecies can be applied'.

Surprisingly, the most recent texts on the fishes of Mongolia (Shatunovskii, 1983 & 1985) make no reference to the revision by Holčík & Skořepa (1971). For the present, the Mongolian representatives of this genus should be referred to the nominate form.

Leuciscus leuciscus baicalensis (Dybowskii, 1874)

Fig. 12

Material. NS 5 & 6, 1986.8.28: 44–48 (136–194 mm); NS 9, 1986.8.28: 49 (166 mm); NS 10 & 11, 1986.8.28: 50–70 (90–147 mm); NS 13, 1986.8.28: 71–75 (29–33 mm); NS 14, 1986.8.28: 76 (166 mm); NS 16, 1986.8.28: 77 (192 mm); NS 36, 1986.8.28: 78 (162 mm); NS 37, 1986. 8.28: 79 (260 mm). Total 36 specimens.

Variation. Lie within the range of meristic characters given by Berg (1948: 77), Holčík & Pivnička (1968: 5) and Shatunovskii (1983: 142).

Geographical range. Restricted to waters of the Arctic basin in Siberia, from the Ob River eastwards to the Kolyma; from their highland headwaters to river mouths.

Ecological notes. Within Mongolia this subspecies is recorded from two rivers in the Arctic basin (Selenga and Shishkid Gols; Shatunovskii, 1983: 143). In addition to these rivers it was also found in the Tamir and Terilg Gol and Ugiy Nuur (see also Dulma, 1979) during the course of this survey.

Taxonomic discussion. The Siberian fauna of *Leuciscus leuciscus* appears to be distinct from other holarctic populations and was recognised subspecifically by Berg (1948) as *L.leuciscus baicalensis*.

Leuciscus idus (Linnaeus, 1758)

Fig. 13

Material. NS 1–4, 1986.8.28: 81–104 (27–143 mm); NS 5–6, 1986.8.28: 105–107 (126–192); NS 7, 1986.8.28: 108–112 (46–83 mm); NS 9, 1986.8.28: 113 (173 mm); NS 10–11, 1986.8.28 :114–116 (94–120 mm); NS 14, 1986.8.28: 117 (186 mm); NS 16, 1986.8.28: 118 (184 mm). Total 38 specimens.

Variation. Lie within the range of meristic characters for this species described by Berg (1948: 97) and Shatunovskii (1983: 144).

Geographical range. Can be considered to have a Eurasian distribution, occurring in Europe from the Rhine and probably the Somme, east-wards to the Siberian Arctic basin as far as the Lena River.

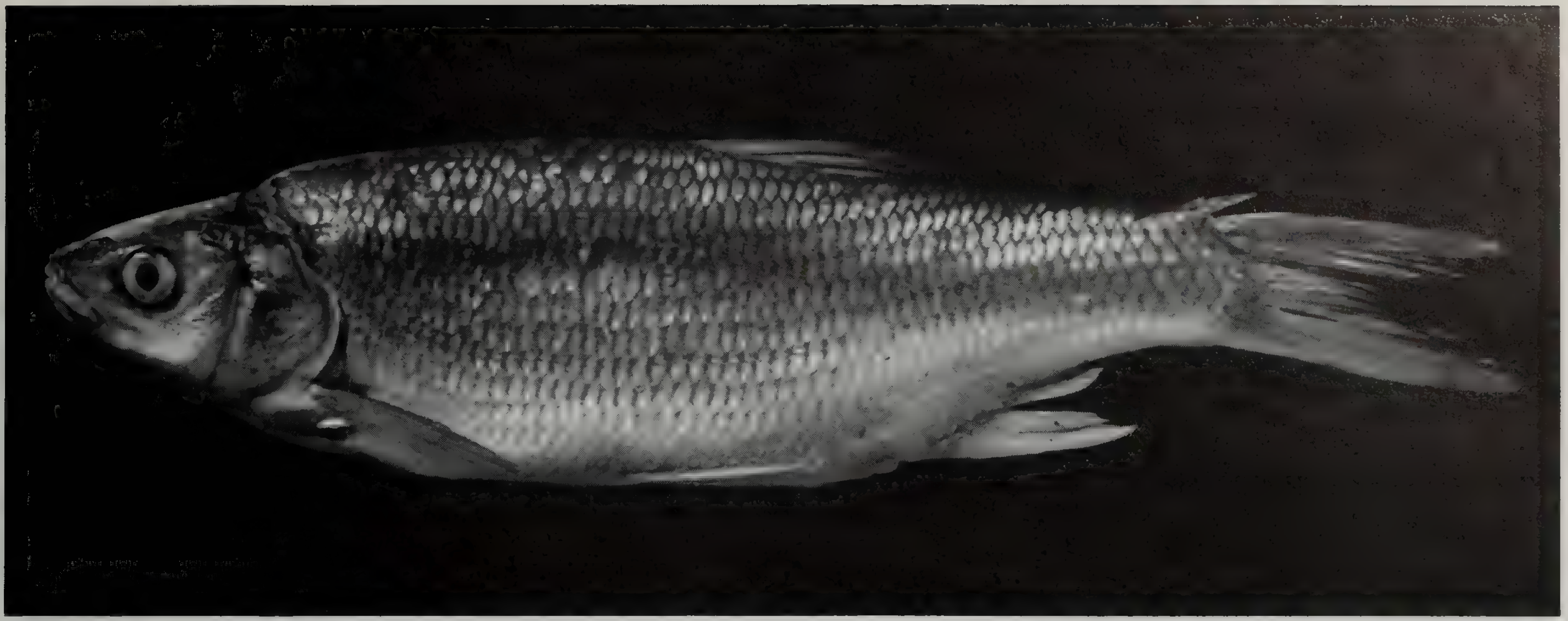


Fig. 13 *Leuciscus idus*, lateral view (192 mm SL: BMNH 1986.8.28: 105–107).

Ecological notes. In Mongolia this species is recorded from waters of the Selenga River basin and was found during this survey in the Tuul Gol and Ugiy Nuur.

Taxonomic discussion. *Leuciscus idus* is distinguished from other Mongolian members of the genus by a greater number of lateral line scales (56–61) and gill rakers (10–14).

Leuciscus waleckii (Dybowskii, 1869)

Material. NS 57; 1986.8.28: 43 (371 mm); NS 44, 1986.8.28: 80 (190 mm). Total 2 specimens.

Variation. Conform to the description supplied by Berg (1949: 102), Holčík & Pivnička (1968: 5) and Shatunovskii (1983: 145; largely taken from Nicholski, 1956: 116).

Geographical range. Distributed within the entire basin of the Amur River system, from upper Mongolian headwaters to the Yalu, Ussuri and Sangari Rivers in eastern China; recorded by Berg (1948: 102) as 'Quite common everywhere . . ' in these waters.

Ecological notes. Within Mongolia *Leuciscus waleckii* is found in rivers and lakes of the Pacific basin and was caught at localities sampled along the Herelen Gol.

Taxonomic discussion. Many meristic characters overlap with those from other *Leuciscus* species, separation may be more easily determined using morphometric data and its alleged endemicity to waters of the Amur basin in Eastern Asia. Live coloration is markedly similar to that of the Siberian roach (*Rutilus rutilus*) with which it can be easily confused.

The large specimen caught during the course of this survey is of a size rarely encountered (Berg, 1948: 102), and has a greater total length than has been previously recorded for the species.

Hitherto, the species was only represented in the collections at the BMNH by a single small specimen collected by V.Brashninov in 1902 and sent as a gift from the museum in Leningrad (BMNH 1925.8.6: 27; previously Leningrad Museum Cat. No. 13851).

Oreoleuciscus potanini Kessler, 1879
'Lake Form'

Fig. 14

Material. NS 22, 1986.8.28: 119–127 (20–30 mm); NS 22, 1986.8.28: 128–140 (16–38 mm); NS 23 & 24; 1986.8.28: 141–152 (115–214 mm); NS 23–24, 1986.8.28: 153–171 (89–213 mm); NS 25–26, 1986.8.28: 172–186 (150–300 mm); NS 25–26, 1986.8.28: 187–192 (269–327 mm); NS 27, 1986.8.28: 193–197 (289–348 mm); RS 2, 1986.8.28: 198–200 (53–86 mm); RS 2, 1986.8.28: 201–247 (10–31 mm); RS 2, 1986.8.28: 248–337 (10–45 mm); RS 2, 1986.8.28: 338–483 (10–37 mm); RS 3–4, 1986.8.28: 484–518 (10–37 mm); RS 3–4, 1986.8.28: 519–581 (12–35 mm). Total 463 specimens.

Variation. Analysis of this material using the diagnosis for three *Oreoleuciscus* species recognised by Berg (1948: 67) and, more recently, Dashdorzh, Dulma and Pivnička (1969) does not lead to a satisfactory allocation of the specimens to any one species. The more recent analyses of Borisovets, Dgebuadze and Ermokhin (1984 & 1985) and Shatunovskii (1985) is adopted here. These authors recognise only a single species, *Oreoleuciscus potanini*, but describe several distinct 'forms'.

Geographical range. *Oreoleuciscus* is endemic to the Central Asian or enclosed Internal basin of Mongolia (Vasil'eva, 1985: fig. 1), with only a small number recorded from the USSR in the upper reaches of the Ob River (Shatunovskii, 1983: 155).

Ecological notes. During the course of this survey, the two localities sampled were the saline lake Boon Tsagaan Nuur and its inflowing freshwater stream Tsagaan Gol (see above, p. 187). Individuals ranging in size from small fry to large mature adults were caught; among them is the largest size recorded for this species (i.e. 348 mm). The lake appeared to support a dense *Oreoleuciscus* population but no other species of fish. Reproductively active males and females, readily shedding their gametes, were taken from several hundred metres off-shore (see p. 187) and contradict the view of Dulma (1979: 726) that these fishes return to freshwater streams and rivers to spawn. Breeding fishes were vividly

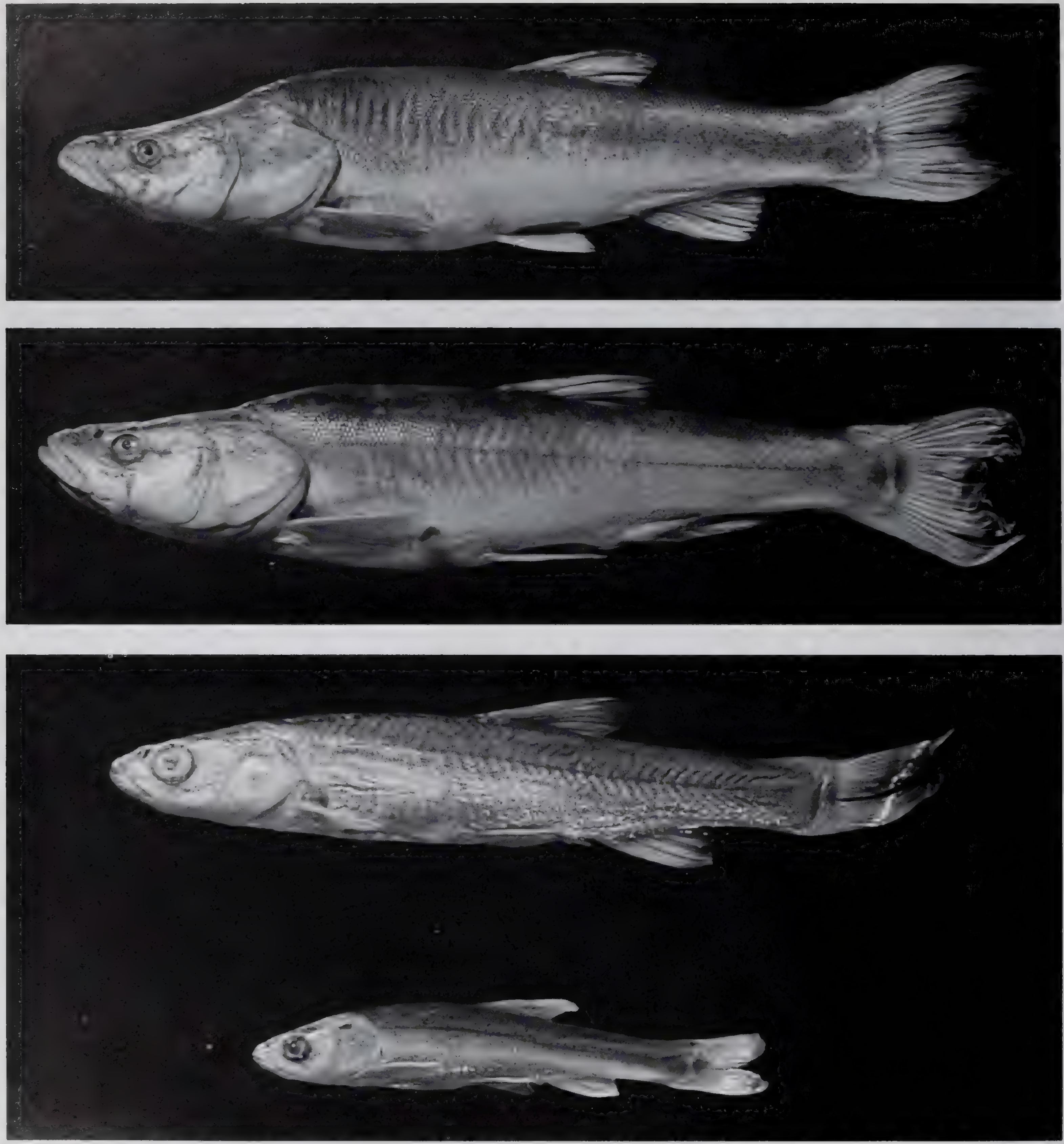


Fig. 14 *Oreoleuciscus potanini* 'Lake Form', lateral view of (Top) gravid female (317 mm SL; BMNH 1986.8.28: 187–192), (Middle) spawning male (300 mm SL; BMNH 1986.8.28: 172–186) and (Bottom) riverine juveniles (86 & 53 mm SL; BMNH 1986.8.28: 198–200).

coloured with a pearly rash on their head (Davies, 1986). Sexually dimorphic females were distinguished by taut abdominal musculature outlining each pair of pleural ribs, hypertrophy of epaxial muscles posterior to the neurocranium, generally elongated snouts and concave dorsal surface of the head. A surprisingly large size range of spawning individuals was collected (e.g. 80–348 mm) and gut contents revealed plant (e.g. algae) and animal (e.g. insect larvae, oligochaetes and smaller individuals of their own species) remains, depending on the fishes' stage of development (see Shatunovskii, 1985: 48).

TAXONOMIC DISCUSSION. The specimens appear to exhibit a combination of many specific characters discussed by Dashdorzh *et al.* (1969). Extensive interspecific variability has led many authors to reassess the composition of the genus. Most recent opinions can generally be divided between the recognition of two closely related but nevertheless distinct

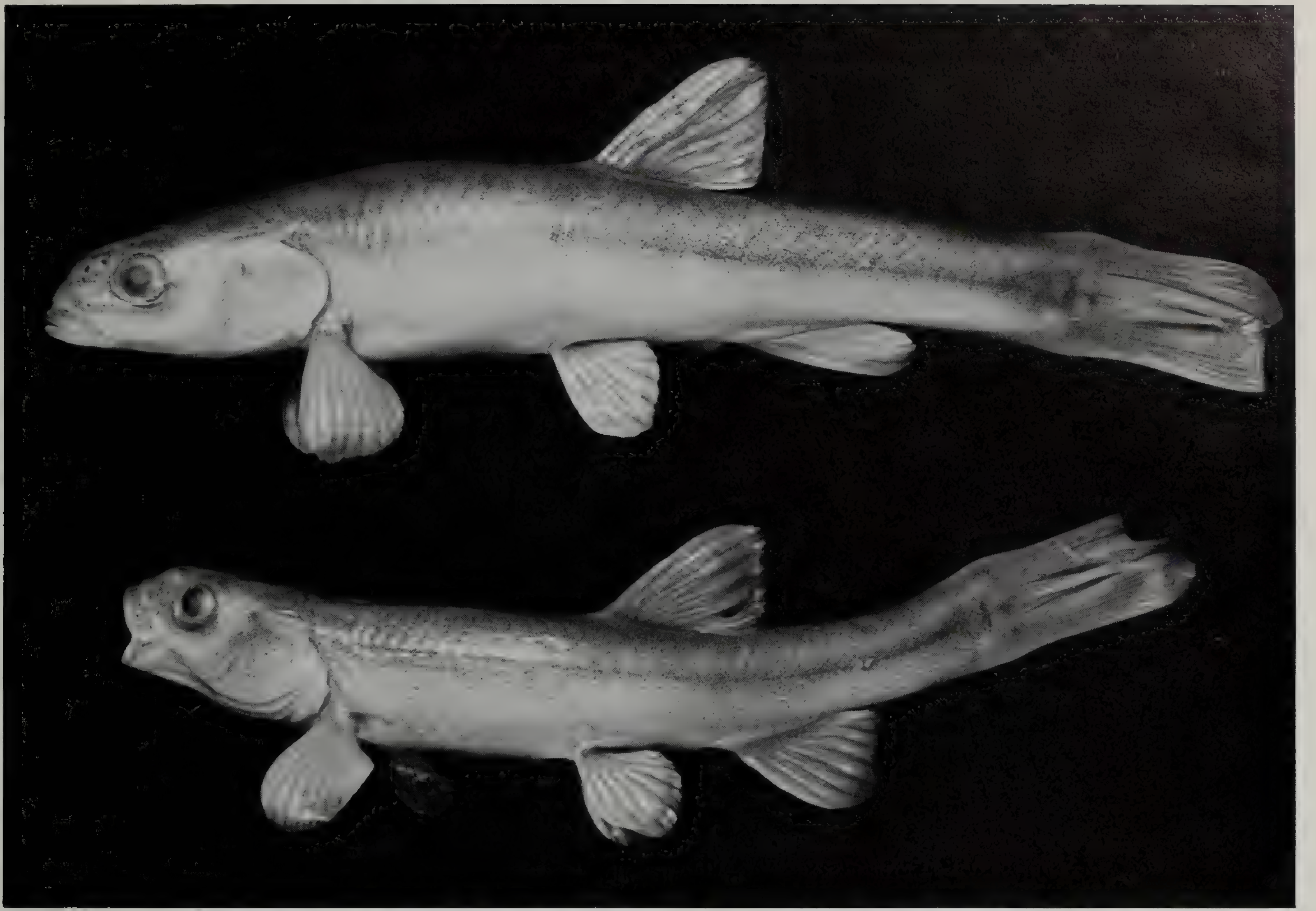


Fig. 15 *Oreoleuciscus potanini* 'Dwarf Form', lateral view (65 & 52 mm SL; BMNH 1986.8.28: 1048–1053).

species (i.e. *Oreoleuciscus potanini* and *Oreoleusicus pewzowi*: Vasil'eva, 1982 & 1985; with judgement being reserved until further analysis of the possibility of a third i.e. *Oreoleuciscus humilis*: after Berg, 1948 and Dashadorzh *et al.*, 1969), or a single polymorphic species (i.e. *Oreoleuciscus potanini*: Jorgansen, 1940; Kafanova, 1961; Svetovidova, 1965; Gundrizer, 1976; Dgebuadze & Ryadov, 1978; Dgebuadze, Ermuhin, Lapin, Ryabov & Trophimenko, 1979; Borisovets *et al.*, 1984 & 1985; Shatunovskii, 1983 & 1985).

'Ichthyophagous', 'phytophagous', 'sharp-snouted' and 'dwarf forms' of the polymorphic *Oreoleuciscus potanini* were described by Shatunovskii (1983), who considered them to occur throughout the water bodies of the Central Asian basin. Borisovets *et al.* (1985) added a 'lake form'. It is confined, together with the 'dwarf form', to the isolated water bodies of the Gobi Valley (i.e. Dolin and Hangiyn systems, see Dgebuadze, 1986, and above), whilst the other forms (i.e. 'ichthyophagus', 'phytophagous' and 'sharp-snouted') are restricted to the water bodies of the Great Lakes Valley (i.e. Kbodo and Dzavkhan River systems: Borisovets *et al.*, 1985; Shatunovskii, 1985; and see above p. 194).

The two distinct *Oreoleuciscus* species recognised by Vasil'eva (1985) were '. . . clearly differentiated' on the basis of only a single character: fusion or segmentation and branching of anterior dorsal fin rays (Vasil'eva, 1985: 31, fig. 2). Analysis of this feature among my specimens from the confined population of Boon Tsagaan Nuur, revealed it to be ontogenetically variable; this seriously diminishes its diagnostic value.

The fishes of Boon Tsagaan Nuur were originally identified by Dashdorzh *et al.* (1969) as *Oreoleuciscus pewzowi*. The morphological variability of the specimens caught during this survey supports the view of a single morphologically plastic species and they are identified as the 'lake form' of *O.potanini*. This species susceptibility to sexual dimorphism or ecophenotypic variation is recognised and associated with ontogenetic stage and reproductive state, or food source and other environmental stresses.

A morphocline of intermediate stages, transitional between the forms described by Shatunovskii (1983) can be clearly recognised and lends support to the view of Borisovets *et al.* (1985) and Shatunovskii (1985) of a distinct 'lake form' in Boon Tsagaan Nuur. This 'form' appears to be present in other Gobi Valley lakes (e.g. Tsatsin Tsagaan Nuur) as specimens collected by the American Museum Asiatic Expedition (see Andrews, 1932 and AMNH specimens 10915, 10918, 11052, 11055, 11057, 11059, 11068, 11094 & 11111) exhibit a similar range of characters.

Unfortunately, I have not had the opportunity to examine *Oreoleuciscus* material from the Great Lakes Valley of Western Mongolia (i.e. the 'ichthyophagous', 'phytophagous' or 'sharp-snouted forms').

Oreoleuciscus potanini **Kessler, 1879**
'Dwarf Form'

Fig. 15

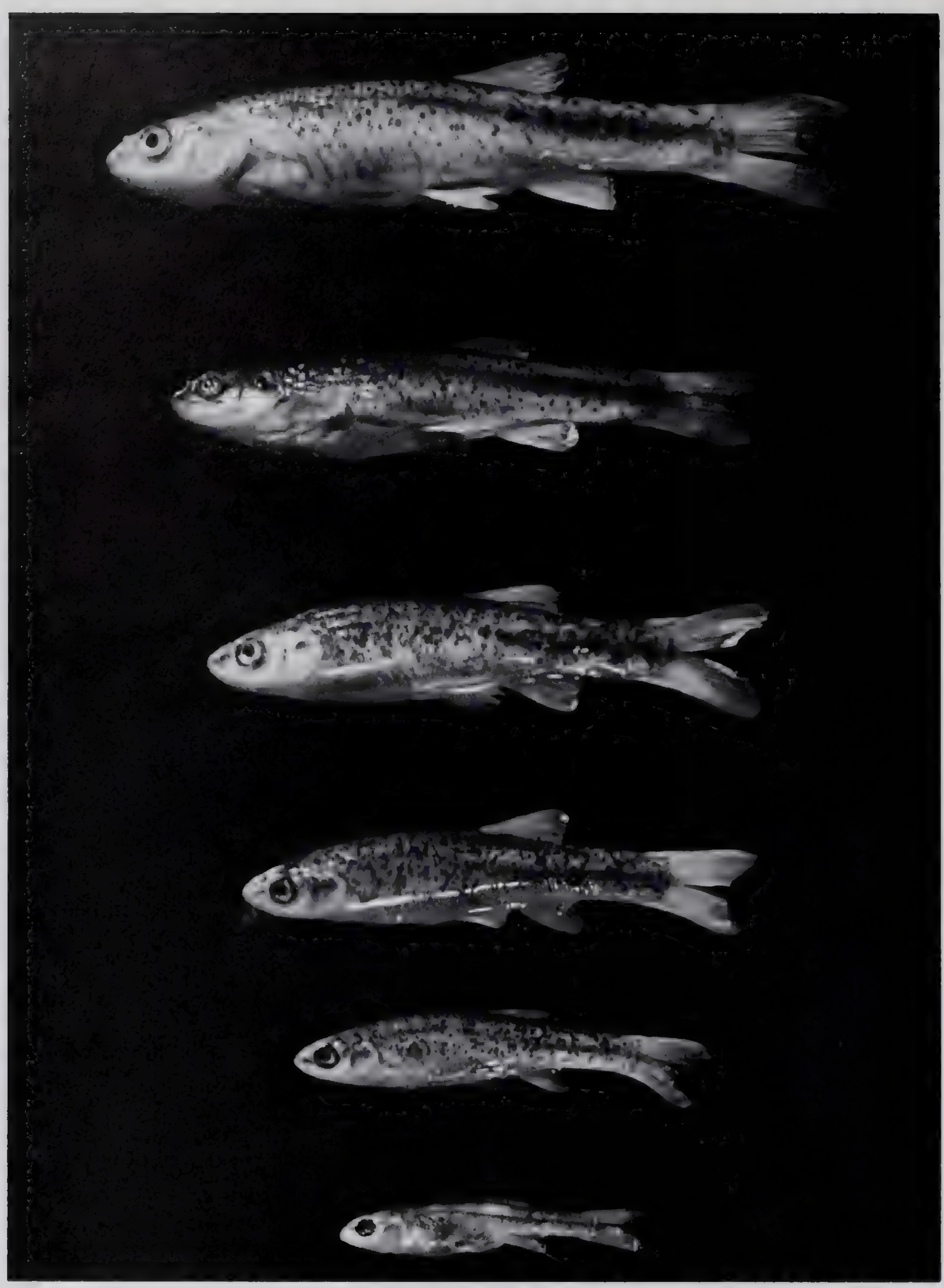


Fig. 16 *Lagowskiella czekanowskii*, lateral views (23–60 mm SL; BMNH 1986.8.28: 820–1045).

MATERIAL. FS 1, 1986.8.28: 1046–1047 (42 & 49 mm); FS 2, 1986.8.28: 1048–1053 (52–65 mm; 1 ex. double stained). Total 8 specimens*.

VARIATION. Conform to the concept of a 'dwarf form' of *Oreoleuciscus potanini* as described by Borisovets *et al.* (1984 & 1985, and see Shatunovskii, 1985).

GEOGRAPHICAL RANGE. Isolated water bodies of the Gobi Valley, Mongolia.

ECOLOGICAL NOTES. These specimens were caught along the shore of Biger Nuur. This small endorheic lake lies several hundred kilometres apart from other water bodies in the western region of the Gobi Valley system and is prone to periodic dessication.

TAXONOMIC DISCUSSION. Superficially these small fishes resemble *Phoxinus*, however, osteological analysis revealed that their long head, nasals and jaws, depressed cranium, somewhat divergent infraorbital canal, well developed supraneurals and exceedingly small scales, all clearly distinguish these taxa. These features are more typical of *Oreoleuciscus* and to some extent *Lagowskiella* as well (see below p. 197 and Howes, 1985), although, my specimens can be distinguished from this genus by a higher number of gill-rakers (12–15) and wider bucco-pharyngeal opening. The striking similarity between the 'dwarf form' of *Oreoleuciscus potanini* and *Lagowskiella* (e.g. *L.czekanowskii* see below p. 197) questions the proposed sister group relationship between this genus and the aspinine cyprinids generally as suggested by Howes (1984).

At the present time *Oreoleuciscus* and *Lagowskiella* are

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* This 'form' of *O.potanini* previously unrepresented in collection of BMNH.

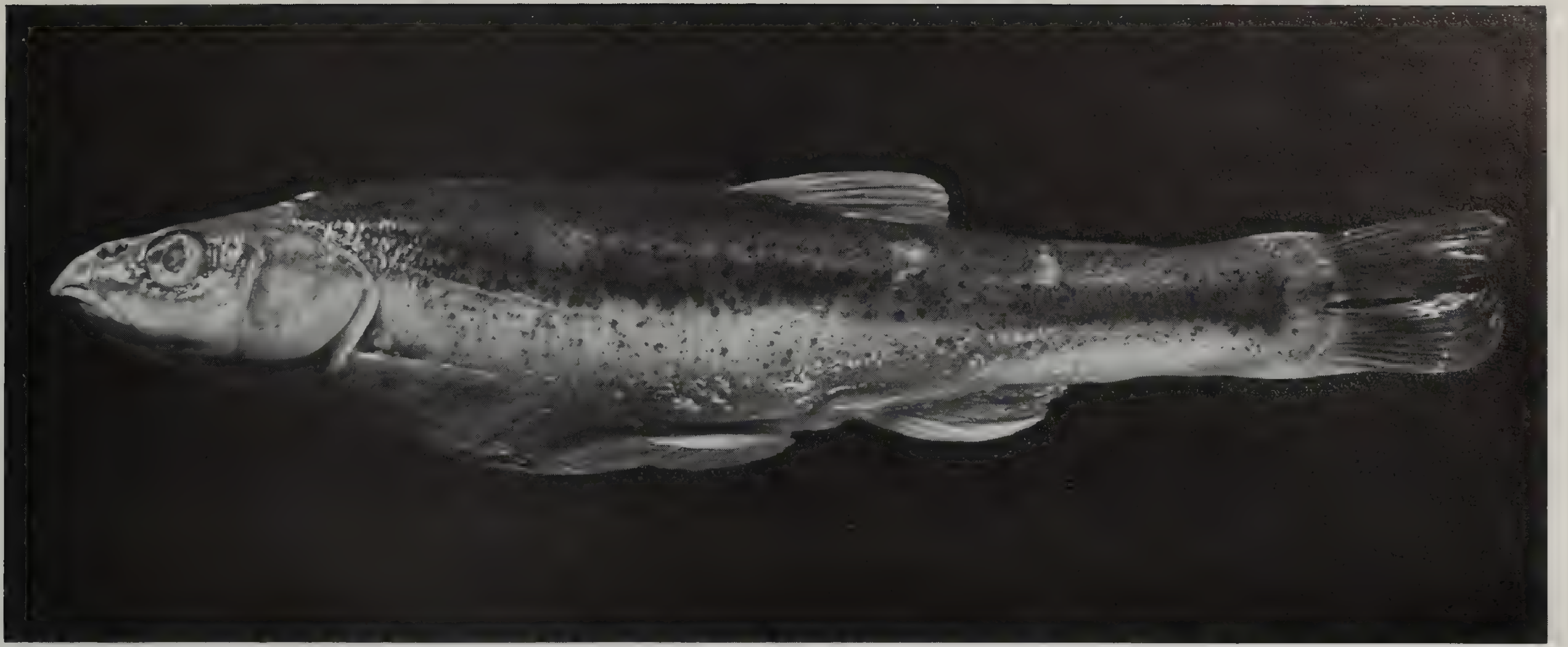

Fig. 17 *Rhynchocypris steindachneri*, lateral view (136 mm SL; BMNH 1986.8.28: 1055).

zoogeographically isolated in distinct drainage basins (Central Asian and Pacific, respectively) which may once have been part of the continuous watershed that extended across central Asia (see earlier section).

The monospecific fish fauna of Biger Nuur and other isolated Gobi Valley lakes make them ideal 'natural laboratories' for investigating epigenetic processes governing ecophenotypic variation or for productivity studies of short, relatively uncomplicated lacustrine food chains.

Lagowskiella czekanowskii Dybowski, 1916

Fig. 16.

MATERIAL. NS 43, 1986.8.28: 796–819 (16–48 mm); RS 7, 1986.8.28: 820–1045 (20–60 mm). Total 251 specimens.

VARIATION. Conform to the diagnosis given by Berg (1948: 117) and Shatunovskii (1983: 161) for *Phoxinus czekanowskii.*

GEOGRAPHICAL RANGE. The Amur River basin including tributaries in northern China, the USSR and eastern Mongolia.

ECOLOGICAL NOTES. Within Mongolia this species appears to be confined to waters of the Pacific basin. During the course of this survey it was collected from inlets and ponds in the flood plain of Herelen Gol. Although Arctic basin localities have been recorded (Berg, 1948; Shatunovskii, 1983: 161), they were for sub-species which cannot be adequately defined by material that is available at present.

TAXONOMIC DISCUSSION. Following the critical analysis by Howes (1985), of genera recognised as synonyms of *Phoxinus* by Berg (1912 & 1948), *Lagowskiella* and *Rhynchocypris* (see below) are accorded separate generic status. In the opinion of Howes (1985: 63) *Lagowskiella* '... shares none of the derived characters that define *Phoxinus*' and, furthermore, can be distinguished by a broader and longer post-orbital region, a more elongate body and posteriorly placed anal fin, several osteological characters, a higher modal vertebral number and an apomorphic gill-raker morphology. He tentatively assigned six species to *Lagowskiella*. *L.czekanowskii* is distinguished principally by its attenuated opercular border and divergent infraorbitals. The morphology of the gill-raker membrane could not be ascertained from the two poorly preserved specimens available to Howes (1985: 67), but has now been examined in these specimens. Their prominent genital papillae are similar to the condition of these organs in *L.lagowskiella* described by Howes (1985: fig. 8).

Rhynchocypris steindachneri (Sauvage, 1883)

Fig. 17

MATERIAL. NS 52–53, 1986.8.28: 1054 (110 mm); NS 56, 1986.8.28: 1055 (136 mm); NS 57, 1986.8.28: 1056 (115 mm). Total 3 specimens.

VARIATION. Lie within the range of morphometric and meristic characters given for this species by Howes (1985: table 1).

GEOGRAPHICAL RANGE. The Amur River basin including tributaries in northern China, the USSR and eastern Mongolia. Its occurrence in Mongolia is recorded here for the first time and extends the known geographical range for the species.

ECOLOGICAL NOTES. Within Mongolia the species is confined to waters of the Pacific basin. The specimens reported upon here were collected from the main stream of the Herelen Gol and a tributary meandering across its flood plain (see above p. 188).

TAXONOMIC DISCUSSION. Three closely related *Rhynchocypris* species were recognised by Howes (1985: 60). This followed his critical review of genera placed in synonymy with *Phoxinus* by Berg (1948) and subsequent authors (e.g. Shatunovskii, 1983 & 1985 and see Howes, 1985: 60 for list of others).

Exclusion of this distinctive taxon from synonymy was based upon the presence of several apomorphic characters, including '... a fleshy rostral process, most highly developed in ripe females (fig. 4), hypertrophied olfactory lamellae with crenate ventral margins, attenuated posterior border of the operculum and a distinct notch on the dorsal border of the

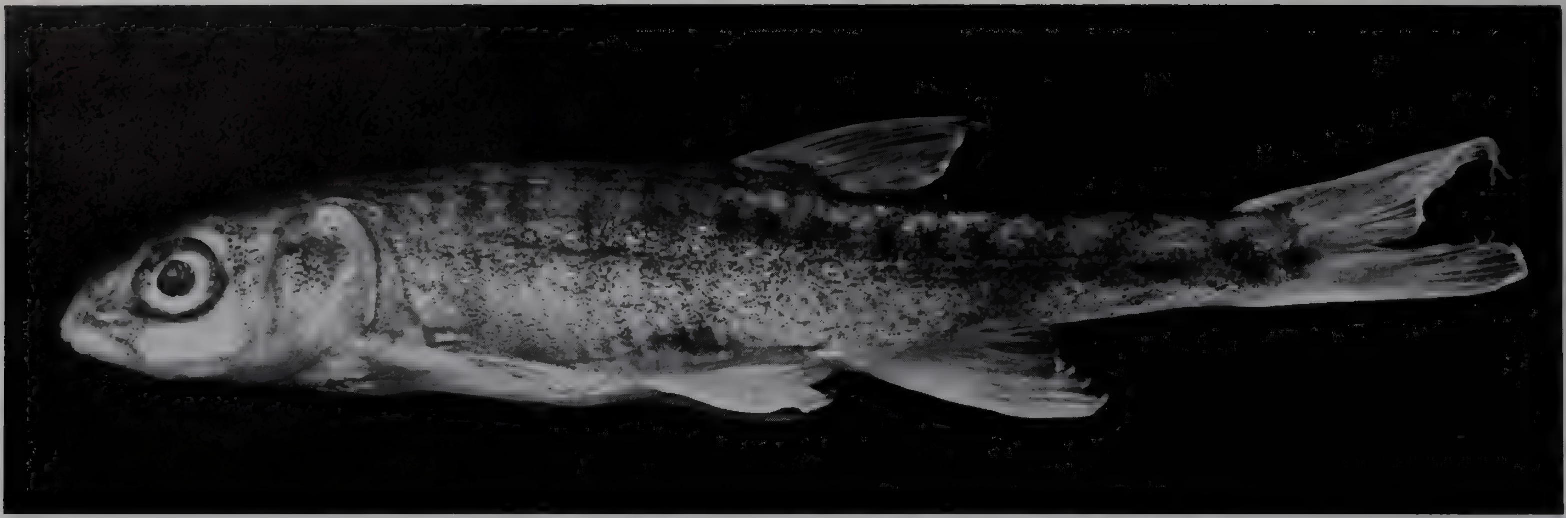

Fig. 18 *Phoxinus phoxinus*, lateral view (54 mm SL: BMNH 1986.8.28: 582–655).

upright part of the cleithral lamellae' (Howes, 1985: 60, fig. 4).

Rhynchocypris steindachneri can be distinguished from its sister species by a shorter head, greater interorbital width and lower scale count. A colour pattern consisting of a dark region around the snout and head that extends posterolaterally as dark mottling overlying a deep lateral band (Howes, 1985: 60, fig. 5a) is also unique to this species. Howes's description was based upon material held at the United States National Museum, Washington and four Japanese specimens in the collections at the BMNH (1907.12.23: 11–14).

Rhynchocypris costatus (Fowler, 1899)

MATERIAL. NS 43, 1986.8.28: 1057 (43 mm); NS 52, 1986.8.28: 1058 (52 mm); RS 7. 1986.8.28: 1059 (40 mm). Total 3 specimens.*

VARIATION. Morphometric and meristic characters conform with those given by Howes (1985: table 1) for this species.

GEOGRAPHICAL RANGE. This species is confined to waters of the Amur River basin. This is the first record from Mongolia and extends the known geographical range of the species.

ECOLOGICAL NOTES. Collected in the main stream and side channels of Herelen Gol.

TAXONOMIC DISCUSSION. *Rhynchocypris costatus* can be distinguished from *R. steindachneri* by a generally more elongate body, longer operculum, and higher vertebral number. The colour pattern consists of a little mottling above a deep lateral band, as described by Howes (1985: 60). His account was based on material in the collection of the AMNH including specimens used by Fowler (1899) for the original description of the species.

Phoxinus phoxinus (Linnaeus, 1758)

Fig. 18

MATERIAL. RS 1, 1986.8.28: 582–655 (12–54 mm); NS 18, 1986.8.28: 656–734 (16–48 mm); NS 32–35, 1986.8.28: 735–786 (25–54 mm); NS 43, 1986.8.28: 787–788 (21–50 mm); NS 56, 1986.8.28: 789–793 (37–43 mm); RS 7, 1986.8.28: 794 (36 mm). Total 213 specimens.

VARIATION. Lie within the range of morphometric and meristic characters given for *P.phoxinus* by Berg (1948), Holčík & Pivnička (1969) and Shatunovskii (1983).

GEOGRAPHICAL RANGE. This widespread Eurasian species is found from the British Isles and France (Wheeler, 1969) across central Europe, the USSR, Mongolia, China and North Korea.

ECOLOGICAL NOTES. In Mongolia is distributed in waters of the Arctic and Pacific basins and was collected during the course of this survey from the Orkhon Gol, Tamir Gol and Herelen Gol (including a little pond in water meadow bordering the main river). The species appears to prefer cold, clear water running over a sand and stone substrate and was often caught together with *Noemacheilus*, *Misgurnus* and young salmonids.

TAXONOMIC DISCUSSION. Since the taxonomic changes proposed by Howes (1985: 71) this is now the only *Phoxinus* found in Mongolian waters. Mongolian species previously allocated to this genus include *P.percnurus*, *P.lagowskii* and *P.czekanowskii* (see Berg, 1948 and Shatunovskii, 1983). Reasons for their exclusion from *Phoxinus* are given by Howes (1985) and these species are now referred to *Eupallasella percnurus*, *Lagowskiella lagowskii* (discussed on p. 197) and *L.czekanowskii* (discussed on p. 197).

Gobio gobio cynocephalus Dybowski, 1869

Fig. 19

MATERIAL. NS 43, 1986.8.28: 1060–1061 (21–22 mm); NS 56, 1986.8.28: 1062 (107 mm); RS 7, 1986.8.28: 1063–1070 (20–32 mm). Total 11 specimens.

VARIATION. Apart from one, all are juvenile and the value of morphometric diagnoses are diminished by ontogenetic variation. The adult specimen (107 mm) lies within the range of morphometric and colour descriptions given by Berg (1948), Holčík & Pivnička (1969) and Shatunovskii (1983).

GEOGRAPHICAL RANGE. This subspecies is recorded in Siberian waters from the Ob and Yenesei Rivers, to the Amur and Liao Rivers in northern China.

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* Species previously unrepresented in collection of BMNH.

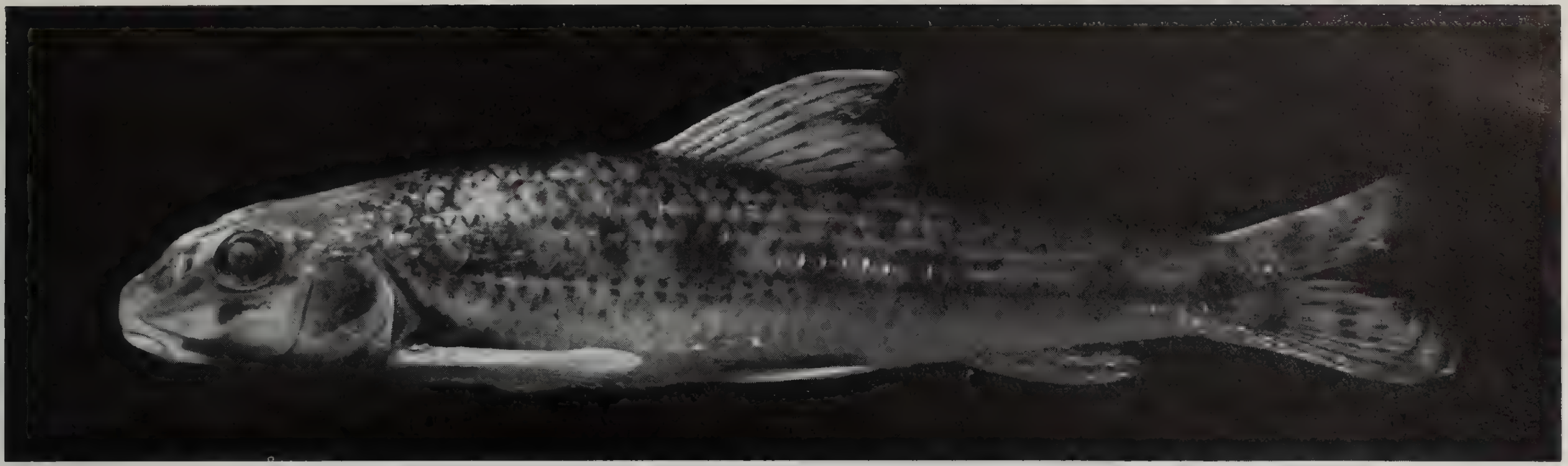

Fig. 19 *Gobio gobio cynocephalus*, lateral view (107 mm SL: BMNH 1986.8.28: 1062).

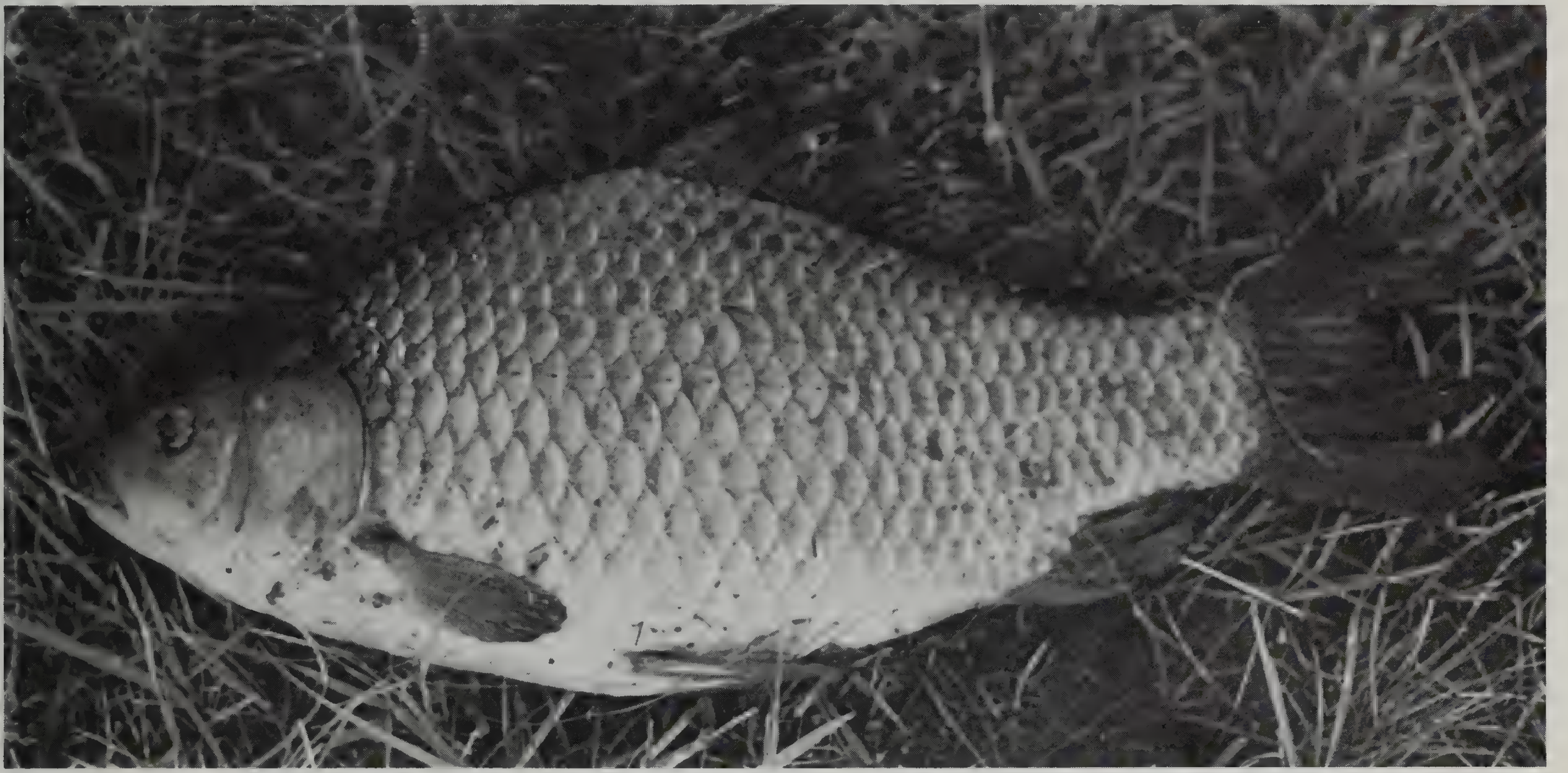

Fig. 20 *Carassius auratus gibelio*, lateral view (306 mm SL; BMNH 1986.8.28: 1071).

ECOLOGICAL NOTES. Within Mongolia is confined to Pacific draining waters and was caught during this survey from Herelen Gol; it is also recorded from the Onon and Khalkhin Gols (Shatunovskii, 1983).

TAXONOMIC DISCUSSION. The largest specimen reported upon here and those recorded by Holčík & Pivnička (1969) contradict the opinion expressed by Shatunovskii (1983) that in Mongolian waters this species only '. . . reaches the length of 6 cm'.

The other *Gobio* species recorded from Mongolia are *G.albipinnatus* and *G.soldatovi*; they are also found in the Pacific basin, but are confined to the Onon and Khalkin Rivers, respectively. *G.albipinnatus* is distinguished by its colourless dorsal fin (Taranets, 1937; Berg, 1948; Holčík & Pivnička, 1969) and *G.soldatovi* by fewer scales in the lateral line and a continuous dark lateral band in place of the distinct series of 8–11 dark spots typical of *G. gobio cynocephalus*.

Hitherto, this subspecies was only represented in the BMNH by three specimens (1898.4.26: 24–26) donated by the Paris Museum in 1898 as part of a collection from Central Asia made by Mr M. Chaffargon.

Carassius auratus gibelio **(Bloch, 1783)**

Fig. 20

MATERIAL. NS 12, 1986.8.28: 1071 (306 mm); NS 57, 1986.8.28: 1074 (95 mm); RS 7, 1986.8.28: 1077–1104 (30–55 mm). Total 30 specimens.

VARIATION. Conform to the description given in Berg (1948: 385) and Shatunovskii (1983 & 1985).

GEOGRAPHICAL RANGE. The natural geographical range of *C.auratus gibelio* extends from eastern Europe to China, although now, it is widespread throughout most of Europe (Wheeler, 1969) and North America (Scott & Crossman, 1973) by introduction.

ECOLOGICAL NOTES. Within Mongolia occurs in Arctic and Pacific drainage systems, in densely vegetated ponds, lakes and slow flowing rivers; caught during this survey in Ugiy Nuur and Herelen Gol.

TAXONOMIC DISCUSSION. Is distinguished from the nominate subspecies by the latter's somewhat larger scales (26–31 in

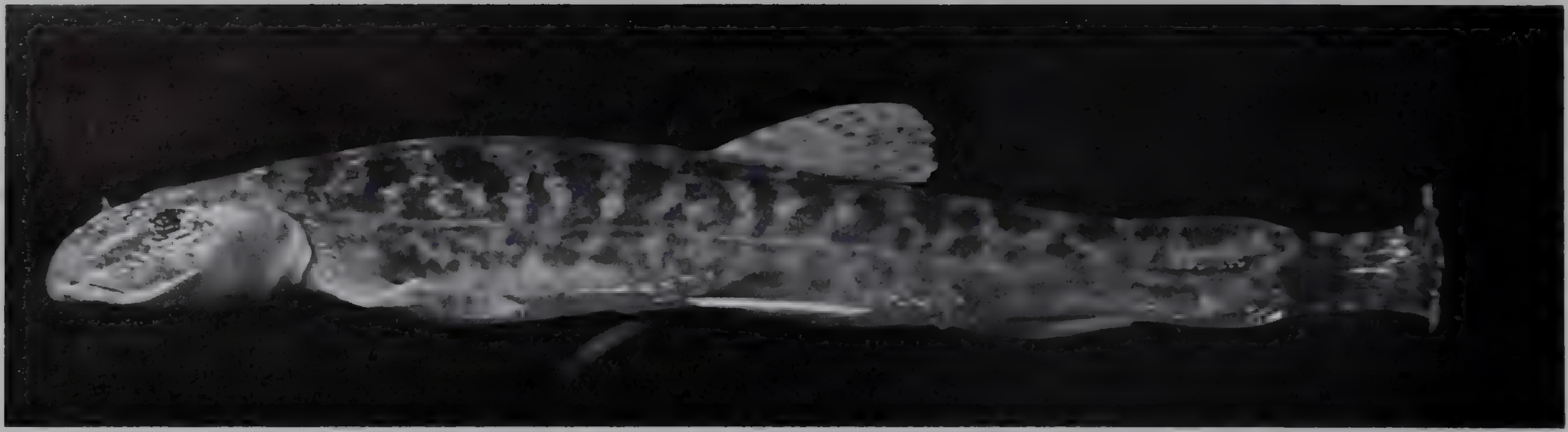

Fig. 21 *Noemacheilus barbatulus toni*, lateral view (100 mm SL: BMNH 1986.8.28: 1167).

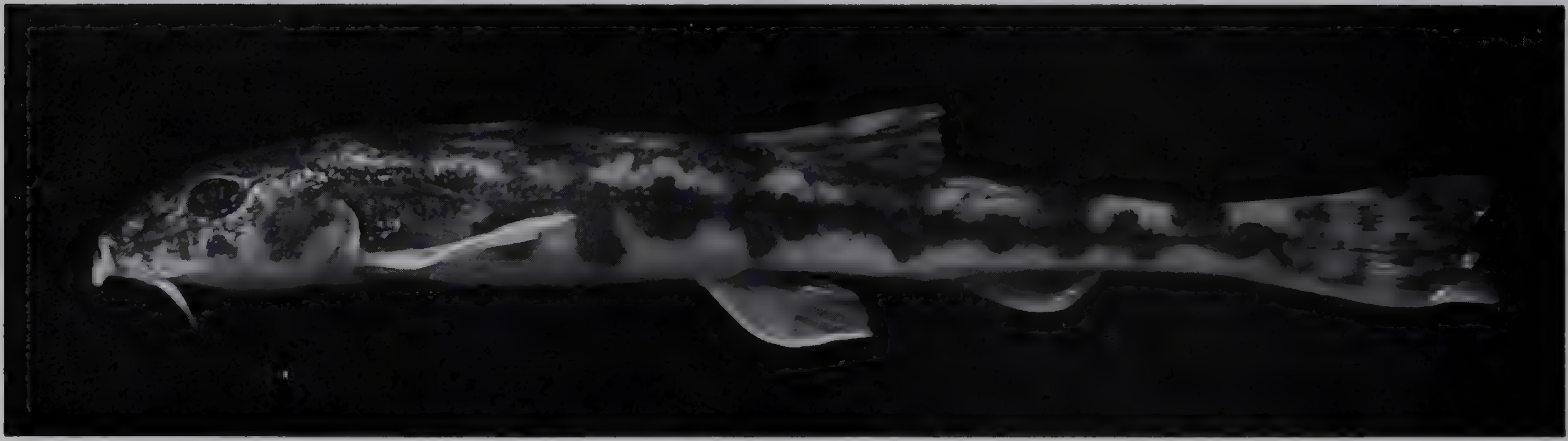

Fig. 22 *Noemacheilus strauchi*, lateral view (50 mm SL; BMNH 1986.8.28: 1171–1178).

lateral line). *Carassius auratus auratus* occurs naturally in Eastern China, the outlying islands Hainan and Taiwan, Korea and Japan. These *C.auratus* subspecies are clearly distinguished from *Carassius carassius* by a higher number of gill rakers on the 1st branchial arch (39–50), fewer lateral line scales (28–31), deeply serrated dorsal and anal fin spines (Berg, 1948: 378, fig. 564 and Wheeler, 1969: 187), usually five branched anal fin rays and a slightly less deep body.

This material joins one specimen (1898.4.26: 23) already deposited in the BMNH from a collection made by Mr M. Chaffargon and three (1905.2.2: 8–11) collected by C. W. Campbell from 'N.E. Mongolia'.

Cyprinus carpio haematopterus (Temminck & Schlegel, 1842)

Material. NS 52–53, 1986.8.28: 1072–1073 (89–91 mm); NS 57, 1986.8.28: 1075–1076 (87–94 mm). Total 4 specimens.

Variation. Conform with the generic diagnosis given by Berg (1948: 390 & 403) and his description of this subspecies (see also Shatunovskii, 1983: 203).

Geographical range. Naturally restricted to Eastern Asia from the Amur River basin through Pacific draining waters of China, Korea and Japan.

Ecological notes. Caught during this survey from Herelen Gol.

Taxonomic discussion. Distinguished from the nominate subspecies by having generally fewer gill rakers on the outer side of the first branchial arch (i.e. 17–25). All specimens caught are juvenile and superficially resemble *C.auratus gibelio*, although close examination revealed the presence of four barbels (2 each side of mouth), a larger base of the dorsal fin and a higher number of lateral line scales (36–39).

Is only the second specimen from this region to be deposited at the BMNH; the first (1905.2.2: 7) was collected by C. W. Campbell.

HOMALOPTERIDAE

Noemacheilus barbatulus toni (Dybowski, 1869)

Fig. 21

Material. RS 1, 1986.8.28: 1105–1108 (25–56 mm); NS 17–18, 1986.8.28: 1109–1112 (30–40 mm); NS 20, 1986.8.28: 1113–1122 (34–90 mm); NS 21, 1986.8.28: 1123–1136 (47–105 mm); NS 32–35, 1986.8.28: 1137–1166 (30–62 mm); NS 37, 1986.8.28: 1167 (100 mm); NS 56, 1986.8.28: 1168 (29 mm). Total 64 specimens.

Variation. Some variation from description given by Berg (1948: 433) considered to be geographically localised and the specimens generally conform to his diagnosis and that of Shatunovskii (1983: 207). These authors are followed here but future attention must be given to pending nomenclatural changes proposed for homalopterid genera (A. C. Wheeler, *pers. comm.*).

Geographical range. Occurs in Siberia from the Ob River eastwards to the Kolyma, Yalu and Liao Rivers in China and is also found in Korea and northern Japan. Sawada (1982: 203, fig. 106) gives a detailed distribution of the genus, which has the widest range of all cobitoid genera.

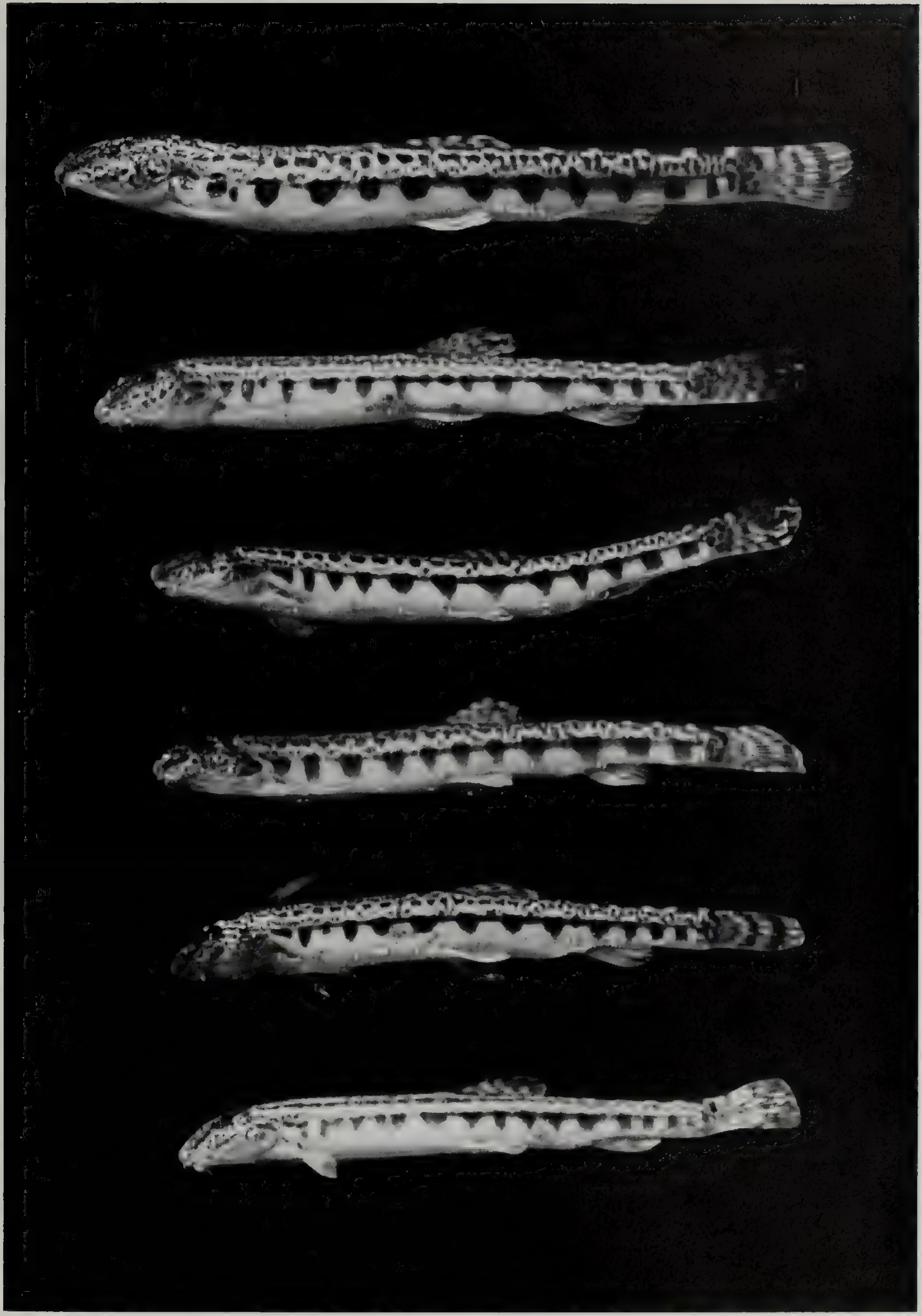

Fig. 23 *Cobitis taenia*, lateral view (53–68 mm SL; BMNH 1986.8.28: 1222–1238).

Ecological notes. In Mongolia it is restricted to waters of the Arctic and Pacific basins (collected from the Orkhon, Tamir, Terilg and Herelen Gol) and is one of two *Noemacheilus* species present.

Taxonomic discussion. The European nominate subspecies (*N. barbatulus barbatulus*; see Sawada, 1982: fig. 93) can be distinguished by the presence of minute scales on the anterior region of its body; they are sparse or entirely absent in *N. barbatulus toni* (Berg, 1948: 422).

Following the revisionary studies of Sawada (1982; see also Parshall, 1983), noemacheiline loaches '... must now be transferred from the Cobitidae to Homalopteridae' (Sawada, 1982: 183) and are given separate subfamilial status: Noemacheilinae.

Noemacheilus comprises more than 100 nominal species. Attempts have been made to subdivide the genus (e.g. Berg, 1948; Bănărescu & Nalbant, 1964, 1966, 1968, 1974 & 1976). Berg's (1948: 411) subgenera *Noemacheilus* (*Deuterophya* and *N.(Noemacheilus)* were based on incomplete versus entire encapsulation of the swim-bladder in an ossified matrix. Further analysis of this character has revealed the existence of a clear morphocline between these two conditions (Sawada, 1982; Parshall, 1983). For the present, in the opinion of Sawada (1982: 202), all species should be retained in *Noemacheilus*. Unfortunately, he did not have access to

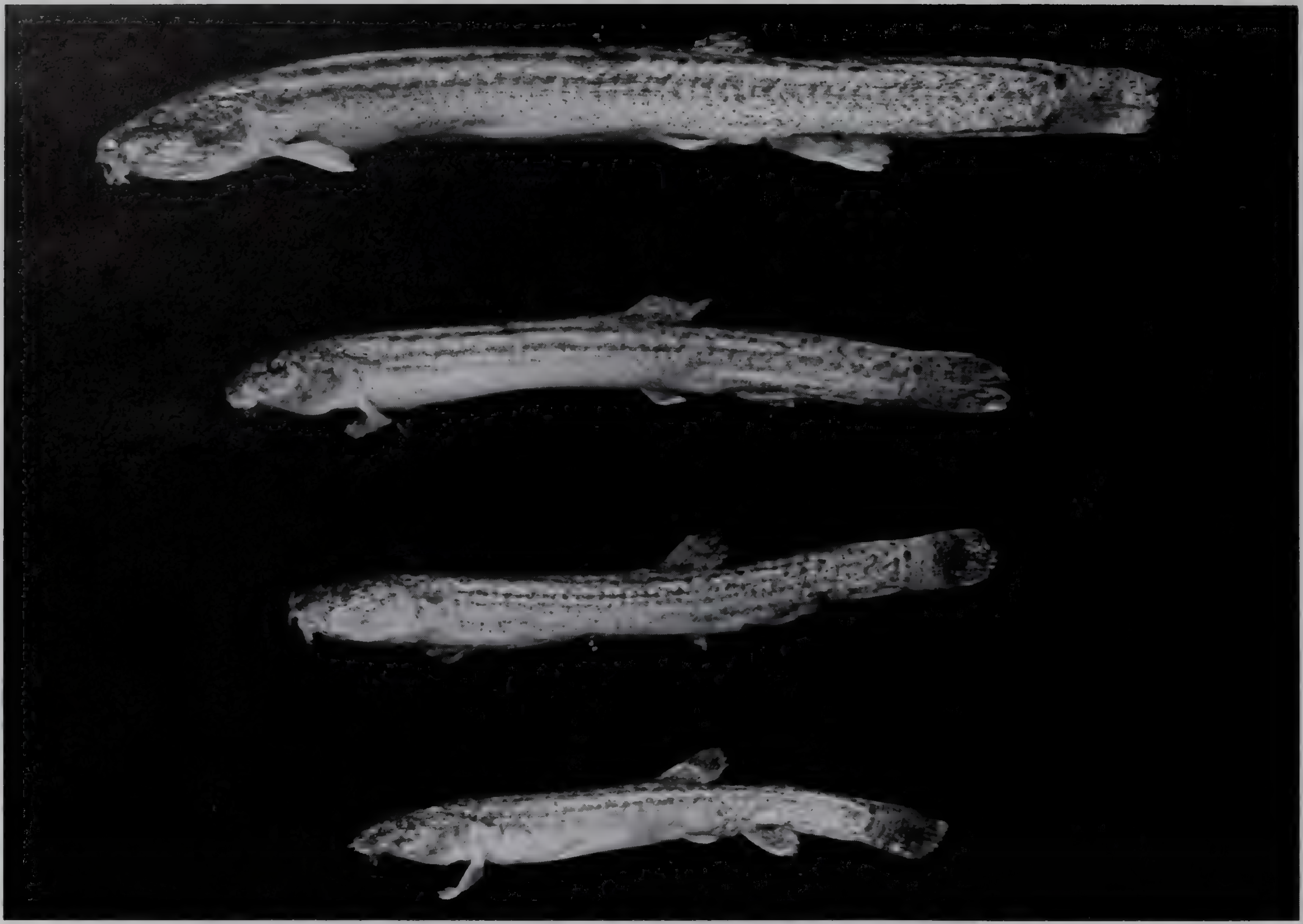

Fig. 24 *Misgurnus anguillicaudatus*, lateral views (32–69 mm SL; BMNH 1986.8.28: 1246–1285).

specimens of the species included by Berg in his *Deuterophysa* (e.g. *Noemacheilus strauchi*, *N.labiatus* or *N.dorsalis*) and their relationships to those distinct *Noemacheilus* lineages tentatively proposed by Sawada (1982: 193, fig. 99) must await future analyses.

Noemacheilus strauchi **(Kessler, 1874)**

Fig. 22

MATERIAL. RS 2, 1986.8.28: 1169–1170 (26–30 mm); RS 3–4, 1986.8.28: 1171–1178 (45–54 mm); RS 3–4, 1986.8.28: 1179–1187 (43–64 mm); RS 3–4, 1986.8.28: 1188–1197 (39–51 mm); RS 3–4, 1986.8.28: 1198–1208 (47–66 mm). Total 40 specimens.

VARIATION. Lie within the range of the descriptions given by Berg (1948: 412), Holčík & Pivnička (1969: 12, figs. 4–7) and Shatunovskii (1983: 210). No specimens were found with a body length exceeding 70 mm. The large sizes recorded by Berg (1948: 412, for specimens from Malyi Saryehegan, Bay of Balkash) were not encountered during this survey.

GEOGRAPHICAL RANGE. Holčík & Pivnička (1969) were first to discover this species in Mongolia and recorded it from '. . . the salt Sangin-dalai lake and Teisingol river'. This locality was also given by Shatunovskii (1983: 210). These isolated water bodies lie within the northern region of the west Mongolian Great Lakes Valley (see p. 179) of the Internal or Central Asian basin. The specimens listed above are the first of this species to be recorded from the Gobi Valley region of the Central Asian basin. Their presence adds support to the faunal uniformity of this zoogeographical province.

ECOLOGICAL NOTES. *Noemacheilus strauchi* was caught in the Tsagaan Gol and tributaries, before this freshwater stream entered the endorheic waters of Boon Tsagaan Nuur; no specimens were caught or observed in the lake waters. It is geographically isolated from the other member of this genus found in Mongolia (i.e. *N.barbatulus toni*) which is confined to the Arctic and Pacific basins.

TAXONOMIC DISCUSSIONS. *N.strauchi* is distinguished from *N.barbatulus toni* by being entirely scaleless and by a portion of its swimbladder lying within the abdominal cavity. The swimbladder is entirely enclosed in a bony capsule in *N. barbatulus toni*, which is also, at least partly, covered in small scales.

The inclusion of this species in *Noemacheilus* must only be retained provisionally. Sawada (1982) has shown that the numerous species presently comprising this genus can be divided into several, apparently monophyletic, lineages.

COBITIDAE

Cobitis taenia **Linnaeus, 1758**

Fig. 23

MATERIAL. RS 1, 1986.8.28: 1209–1215 (40–58 mm); NS 17–18, 1986.8.28: 1216–1220 (49–72 mm); NS 20, 1986.8.28: 1221

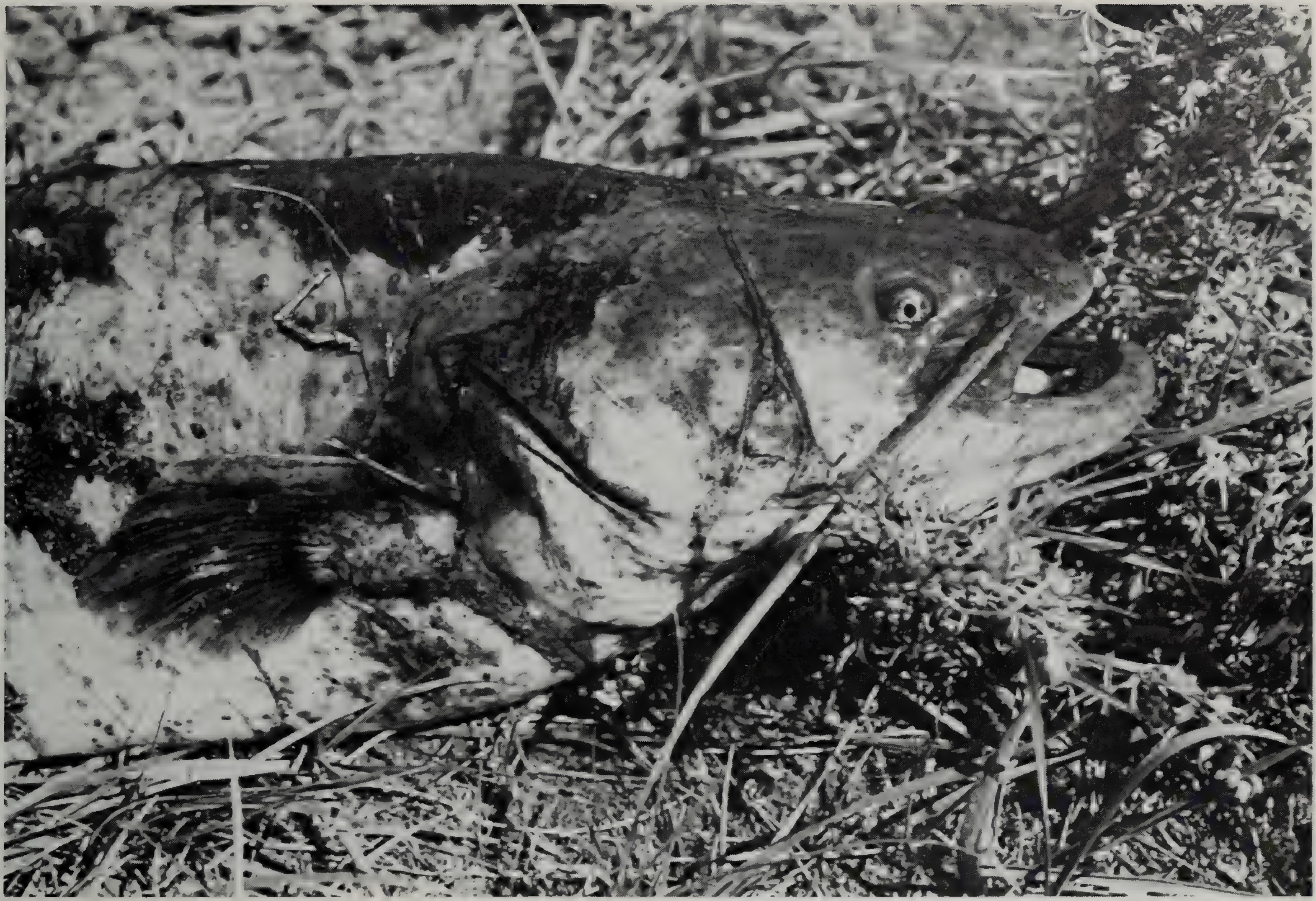

Fig. 25 *Silurus asotus*, lateral view of head region (665 mm SL; BMNH 1986.8.28: 1287).

(56 mm); NS 32–35, 1986.8.28: 1222–1238 (53–73 mm); NS 43, 1986.8.28: 1239–1244 (52–79 mm); NS 56, 1986.8.28: 1245 (60 mm). Total 37 specimens.

VARIATION. Morphometric and meristic characters conform to the descriptions in Berg (1948: 455) and Shatunovskii (1983.)

GEOGRAPHICAL RANGE. Widespread Eurasian species, ranging from western Europe (Wheeler, 1969) to the eastern China seaboard (Nichols, 1943); see Sawada (1982: 199, fig. 103) for detailed distribution of the genus.

ECOLOGICAL NOTES. Within Mongolia is confined to waters of the Arctic and Pacific basins; in flowing and stagnant waters with silty and muddy substrate. Caught during this survey in Orkhon Gol, Tamir Gol, Terilg Gol and Herelen Gol.

TAXONOMIC DISCUSSION. A Siberian subspecies (Gladkov, 1935) in which head length is equal or only slightly longer than the caudal peduncle (Berg, 1948: 459), can be clearly distinguished from *Cobitis taenia* in which head length far exceeds caudal peduncle length.

Misgurnus anguillicaudatus (Cantor, 1842)

Fig. 24

MATERIALS. NS 43, 1986.8.28: 1246–1285 (20–81 mm); RS 7, 1986.8.28: 1286 (36 mm). Total 41 specimens.

VARIATION. Conform to the description in Berg (1948: 467).

GEOGRAPHICAL RANGE. Is confined to the basin of the Amur River.

ECOLOGICAL NOTES. In Mongolia is found only in Pacific draining waters. It was caught during this survey in tributaries and ponds of the Herelen Gol.

TAXONOMIC DISCUSSION. This species was considered to be subspecifically distinct from the taxon *M.fossilis* by Nicholski (1956); a view adopted by Shatunovskii (1983: 213). However, Sawada (1982) retained them as two distinct species on the grounds that they exhibit unique osteological characters. His distinction is followed here, although it is recognised that the species within this genus are in need of revision. The discontinuous geographical range of the genus is given by Sawada (1982: 198, fig. 102).

SILURIDAE

Silurus asotus Linnaeus, 1758

Fig. 25

MATERIAL. NS 12, 1986.8.28: 1287 (665 mm). Total 1 specimen.

VARIATION. Conforms to the description of this species given in Berg (1948: 475), Holčík & Pivnička (1969: 16) and Shatunovskii (1983: 214–216 & 1985: 151).

GEOGRAPHICAL RANGE. This species is the only catfish recorded from Mongolia and was considered by Berg (1948:

475) to be confined to waters of the Amur basin. However, Dulma (1979: table 3) listed it among species found in lakes within the Arctic basin as well.

ECOLOGICAL NOTES.During the course of this survey, the species was caught in Ugiy Nuur. This confirms its presence outside the Amur basin and a distribution within Mongolia extending across Arctic as well as Pacific draining waters.

Gut contents analysis revealed the diet of this piscivorous species in Ugiy Nuur to be juvenile *Perca* and *Leuciscus*. A single juvenile *Perca* (40 mm) was found in the stomach of the preserved specimen reported upon here. A prominent genital papilla is also exhibited by this specimen.

TAXONOMIC DISCUSSION. Berg (1948) and most subsequent authors followed the reallocation of the species to the genus *Parasilurus*. This was originally suggested by Bleeker (1862: 393) largely on the basis of it possessing only two pairs of barbels in place of three in most *Silurus* species. Haig (1952) revised the Oriental and Palaearctic Siluridae and analysed this and other characters used to separate these genera. She concluded that 'It does not seem advisable to separate genera on the basis of a character which is dependent upon physiological growth factors. Especially . . . since it can be shown that in small populations of usually 4-barbelled forms, a few individuals may appear with 6 barbels.' In coming to this conclusion based on the ontogenetic variability of barbel numbers, Haig (1952: 72) cited the work of several earlier authors including Atoda (1935), Kimura (1935), Hora (1936) and Bhimachar & Rau (1941).

Berg (1948: 476) noted the presence of three pairs of barbels in larval *Silurus asotus* (as described by Soin, 1947) but considered the adult condition adequate to define a distinct genus. However, his descriptions do not reveal any character that is unique to *Parasilurus*. He even noted that the smooth pectoral fin spines are prone to vary intraspecifically thereby diminishing the value of this character. The synonymy of *Parasilurus* as proposed by Haig (1952) is, therefore, upheld and the Mongolian silurid catfish recognised as *Silurus asotus*

Previously this species was represented in the BMNH by a single specimen collected by Mr M. Chaffargon (1898.4.26: 9) from the Herelen Gol and another collected by C. W. Campbell (1905.2.26: 6) from 'N.E. Mongolia'.

GADIDAE

Lota lota (Linnaeus, 1758)

MATERIAL. NS 40, 1986.8.28: 1288 (376 mm); NS 41, 1986.8.28: 1289–1290 (257–289 mm); NS 56, 1986.8.28: 1291 (180 mm). Total 4 specimens*

VARIATION. Conform to the descriptions and range of morphometric and meristic characters given for the species by Berg (1948), Holčík & Pivnička (1969: 18), Wheeler (1969: 283), Scott & Crossman (1973: 641–645) and Shatunovskii (1983: 216–218 & 1985: 158–161).

GEOGRAPHICAL RANGE. This monotypic genus is distributed in the freshwaters of North America and continental Eurasia, from western France, the eastern region of England (where the lack of reliable, recent records suggests that it may now be extinct), across the USSR to the Amur River and its southern Chinese tributaries (Berg, 1948; Wheeler, 1969; Scott & Crossman, 1973).

ECOLOGICAL NOTES. In Mongolia *Lota* is widespread throughout rivers and lakes (see Dulma, 1979: table 3) in the Arctic and Pacific draining waters and was caught during this survey in representative localities (i.e. Tamir Gol and Herelen Gol) from both basins. Analysis of their gut contents revealed a predominance of caddis fly larvae, molluscs and leeches amongst general debris of aquatic insects, plant material and small stones; these suggest a benthic feeding habit. The gut was particularly densely packed in the two medium sized specimens; the smaller (257 mm) containing twelve leeches (up to 15 mm long) and the larger (289 mm) numerous densely packed caddis fly and other larvae. This supports the view that *Lota* is a voracious predator and night feeder. However, no fish remains were detected even in the largest specimen (376 mm).

TAXONOMIC DISCUSSION. Two subspecies were thought to occur in North America (Hubbs & Schultz, 1941) and parts of north-eastern Siberia (Berg, 1948). However, in the opinion of Scott & Crossman (1973: 642) '. . . in the present state of our knowledge, the recognition of subspecies seems unwarranted.'

PERCIDAE

Perca fluviatilis Linnaeus, 1758

Fig. 26

MATERIAL. NS 5–6, 1986.8.28: 1292 (310 mm); NS 7, 1986.8.28: 1293–1352 (33–55 mm); NS 10–11, 1986.8.28: 1353 (222 mm); NS 13, 1986.8.28: 1354–1403 (31–47 mm); NS 14, 1986.8.28: 1404 (244 mm); NS 15, 1986.8.28: 1405–1406 (149–158 mm). Total 115 specimens.

VARIATION. Conform to descriptions in Berg (1948: 105), Wheeler, (1969: 322) and Shatunovskii (1983: 218 & 1985: 161).

GEOGRAPHICAL RANGE. This species has a wide Eurasian distribution continuous from France and England eastwards across continental Europe and the USSR to northern Mongolia (Collette & Bănărescu, 1977).

ECOLOGICAL NOTES. Is confined in Mongolia to the Arctic drainage basin and was found to be abundant in Ugiy Nuur, see Dulma (1979: table 3) for further localities of this principally lacustrine species. It is absent from the Amur River system and Pacific draining waters of Mongolia.

This predatory species is carnivorous and often cannabalistic as shown by gut contents analysis of the largest specimen (310 mm); it contained 17 juvenile perch ranging in size from 4 or 5 to 30 mm.

TAXONOMIC DISCUSSION. The perch of North America (*Perca flavescens*) has long been considered a distinct, albeit closely related species. However, Svetovidov & Dorofeeva (1963) concluded that there is only a single circumpolar species. Their conclusion was supported by Thorpe (1977); following extensive morphological, physiological, ecological and behavioural comparisons he concluded, from '. . . overwhelming

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* These four specimens represent the first from Asian waters to be deposited at the BMNH.

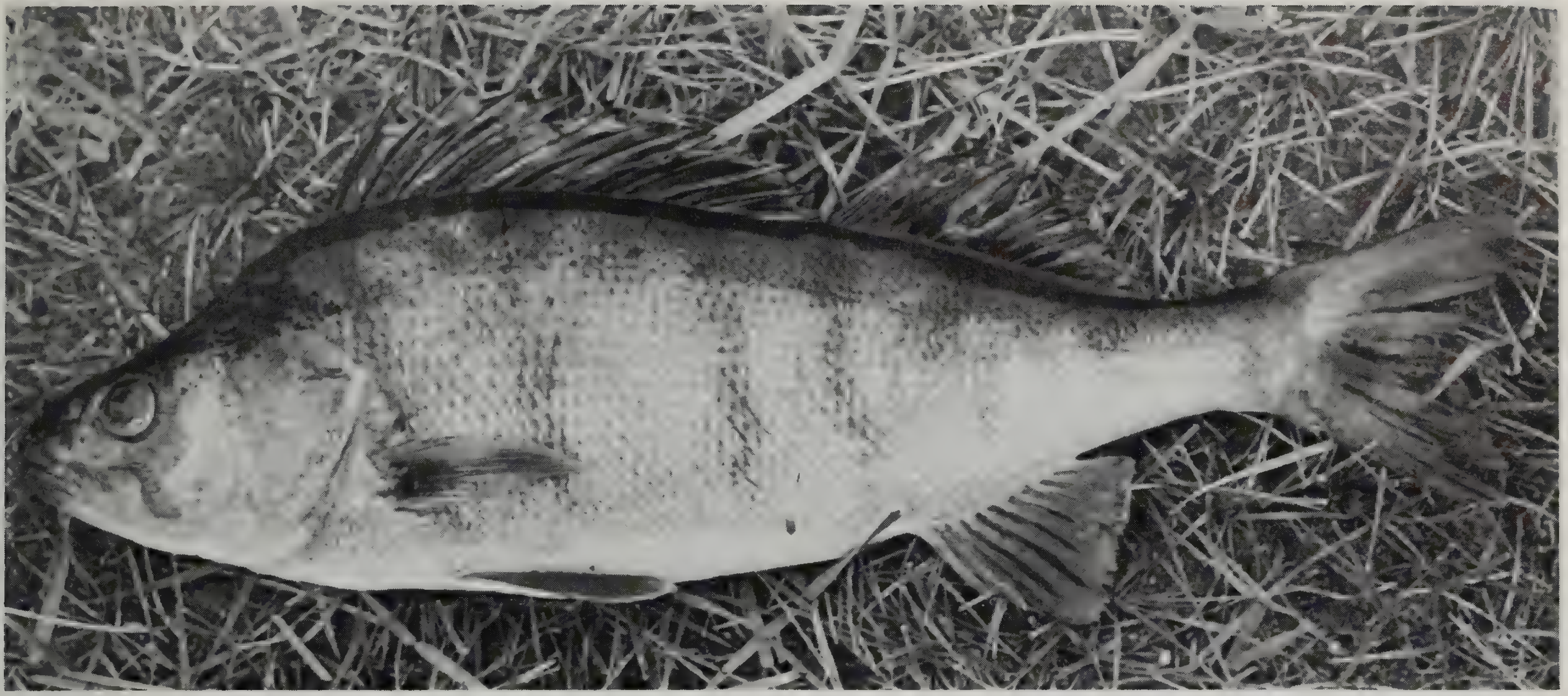

Fig. 26 *Perca fluviatilis*, lateral view (244 mm SL; BMNH 1986.8.28: 1404).

similarities ... it seems prudent to regard the two fishes as functionally the same.' This proposed synonymization has not been unanimously accepted (e.g. see Scott & Crossman, 1973: 756). Most recently, Collette & Bănărescu (1977) have found a morphological character (position of the predorsal bone) by which the two species can be invariably distinguished and cite this and a number of additional characters to '... verify the validity of *P.flavescens*'.

ACKNOWLEDGEMENTS. This study was undertaken with the aid of a Mongolian Government Scholarship awarded jointly by the British Council and Mongolian People's Republic. I acknowledge with thanks assistance given by Dr. Chris Gamble and her colleagues in the Eastern Asia Department of the Council.

It is with great pleasure that I thank members of the Mongolian State University and Ministry of Foreign Affairs who sponsored my visit, for their warm hospitality during the course of my stay and for arranging access to remote regions of their country. In particular I thank Prof. Tsendsuren of the Department of Zoology, Mongolian State University, and staff members Dashzoolk and Damdinsuren for valuable help and companionship in the field. My sincere thanks also to Prof. A. Dulma, Head of the Department of Biology, Mongolian Academy of Sciences, for useful discussion and a generous gift of specimens from Biger Nuur. Translator Altangerel is also gratefully acknowledged for his help and friendship.

Support given by British Embassy staff in Ulan Bator was invaluable, in particular I thank Ambassador James Paterson and First Secretary Nick Haycock and their kind families.

For assistance in various ways special thanks are also extended to Dr K. E. Banister, Prof. C. Bawden, Prof. R. Billard, A. O. Chater, E. J. Copley, Dr Jon Davies, Alain Desjaque, Dr G. Fryer FRS, Dr P. H. Greenwood FRS, Dr J. S. (Pat) Heslop-Harrison, Prof. A. Hoyes, Dr C. Humphrey, The Earl Jellicoe and Dr W. Nixon and family. The late Hon. Ivor Montagu is also remembered for his early advice and encouragement.

For loans, information or access to material in their care I thank Dr M. -L. Bauchot (Museum National d'Histoire Naturelle, Paris), Dr B. Coad (National Museum of Natural Sciences, Canada) and Dr G. Nelson (American Museum of Natural History).

I acknowledge with gratitude the Trustees of the British Museum (Natural History) and Keeper of Zoology for access to the collections and research facilities; with special thanks to my colleagues in the Fish Section, particularly Alwyne Wheeler and Gordon Howes for valuable discussion and criticism of the text.

Finally, special thanks to my family especially Kath for the tolerant support and encouragement that made this possible.

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Manuscript accepted for publication 12 July 1988

Bull. Br. Mus. nat Hist (Zool.) **55**(2): 209–257 Issued 26 October 1989

Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology.

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SYNOPSIS. Relationships of lacertid lizards were assessed on the basis of 84 primary and 112 binary characters drawn mainly from morphology, including features of the skeleton, external anatomy, various internal soft part systems and two aspects of behaviour. Among features not previously used, or not fully investigated before, are structure of the septomaxilla and nasal passages, arrangement of the xiphisternal cartilages, mite pockets, kidney position, ulnar nerve arrangement, thoracic fascia, aspects of the hemipenis and its associated muscles, female genitalia and jaw muscles. On the basis of parsimony analysis and compatibility treatment of this character set, the Lacertidae fall into two main portions: a paraphyletic Palaearctic and Oriental group of primitive forms, from which is derived a holophyletic assemblage of Ethiopian and advanced Saharan and Eurasian taxa.

The former group is not fully resolvable, but *Psammodromus* and *Gallotia* appear to be sister groups and are probably related to *Lacerta parva* and *L. fraasi* and then *L. brandtii*. *Podarcis* appears to be related successively to *L. andreanszkyi*, the sister species *L. dugesi* and *L. perspicillata*, and perhaps *L. danfordi* and *L. laevis*. This assemblage may be related to archaeolacertas and *Algyroides*. The separation of *Lacerta lepida, L. pater* and *L. princeps* from the *L. agilis* group, based on chemical evidence, is weakly contradicted by morphology. *Takydromus* may be most closely related to *L. vivipara*, and *Lacerta jayakari* and *L. cyanura* constitute the most likely sister group of the Ethiopian and advanced Saharo-Eurasian assemblage.

Taxa in the Ethiopian and advanced Saharo-Eurasian assemblage form a long essentially pectinate tree with relatively minor change between the side branches, except for a strong disjunction separating the more primitive from the more advanced taxa. Most of the former fall on two main branches, with *'Lacerta' australis* and *'L.'rupicola* possibly basal to them. 1. the Equatorial forest group containing *Gastropholis, Bedriagaia, 'Lacerta' echinata, Adolfus, 'Lacerta' jacksoni* and *Holaspis*. The first three of these constitute a holophyletic group and the same is probably true of the remainder. 2. *Tropidosaura, Poromera* and *Nucras*, the latter being the sister group of the more advanced forms. These include successively the Ethiopian *Philochortus, Latastia, Ichnotropis* and *Heliobolus, Pseuderemias, Meroles* and *Aporosaura*, and *Pedioplanis*, and then the Saharo-Eurasian *Eremias, Acanthodactylus, Mesalina* and *Ophisops-Cabrita*.

It seems probable that the ancestors of modern Lacertidae arose in western Eurasia, where the family is known since the Palaeocene and is still represented there largely by quite primitive forms (89 species and seven nominal genera). The family later invaded Africa, perhaps first in the early or middle Miocene. Relatively primitive lacertids spread widely in largely mesic situations in the Ethiopian region, radiating to some extent (six present genera and 16 species) and producing *Nucras* and the related series of advanced groups (eight genera and 54 species) which show increasing adaptation to xeric environments. These genera tend to have their most primitive species in the northeast and north of the Ethiopian region. The most advanced gave rise to the Saharo-Eurasian clade, now made up of *Eremias, Acanthodactylus, Mesalina* and *Ophisops-Cabrita*. This invaded the arid areas of North Africa and Eurasia, where it is presently represented by 70 species. Many morphological changes in increasingly advanced lacertids may be functionally related to the problems of survival in arid, hot, open environments. Considerable ecological parallelism exists in lacertids, with members of separate stocks occupying similar niches in different geographical areas. Morphological adaptations associated with these niches contribute significantly to the high levels of character homoplasy found in the family. There is also some correlation between the degree of niche differentiation in various groups and the quality of the phylogenies that can be produced from their physical characters. A number of morphological parallels exist between advanced lacertids and New World macroteiids. In the skull at least, advanced lacertids show a complex mixture of paedomorphosis and acceleration.

Nomenclatorial changes are as follows: *Cabrita* is synonymised with *Ophisops*, necessitating a new name, *Ophisops nictans*, for *Cabrita jerdonii*. *Aporosaura* is synonymised with *Meroles, Platyplacopus* with *Takydromus*, and *Bedriagaia* with *Gastropholis*. *'Lacerta'* (or *Centromastyx*) *echinata* is also transferred to the latter genus and *Lacerta jacksoni* to *Adolfus*. *'Lacerta' australis* and *'L'. rupicola* are put in a new genus, *Australolacerta*. It is recommended that *Lacerta dugesii* and *L. perspicillata* should not be placed in the otherwise very uniform genus *Podarcis*. Although clearly paraphyletic, *Lacerta* s. lat. should be retained at least for the present and, if necessary, putative relationships within it indicated by informal groups or subgenera.

INTRODUCTION

The Lacertidae are one of the few large or medium-sized families of lizards not to have been subjected to some form of overall phylogenetic analysis in recent years. The last general treatment was that of G. A. Boulenger (1920, 1921) in his monumental *Monograph of the Lacertidae** which was based almost entirely on external features of the lizards. As these seem to be subject to considerable parallel evolution, I have attempted to widen the available character base by including features of the skeleton and various soft-part systems, such as the nasal tract, kidney, jaw and cloacal muscles, hemipenis and female genitalia. Some of these features have also been discussed elsewhere (Arnold, 1973, 1983, 1984, 1986*a*, 1986*b*, 1986*c*). Julien and Renous-Lécuru's (1972) work on the ulnar nerve is incorporated and extended and two behavioural characters are included. Recent investigations in the fields of karyology and the immunology and electrophoresis of blood and tissue proteins are also considered. Analysis has been carried out using 112 binary characters and 44 taxonomic units that are likely to be holophyletic. These have been subjected to both parsimony and compatibility treatments.

There are over 230 species of lacertid lizards, presently assigned to about 27 genera (see p. 211). They are distributed through most of Eurasia and all of Africa. A few species occur on some off-shore islands, including the British Isles, the Canaries, Madeira, many Mediterranean islands, Socotra, Sri Lanka, Sumatra, Borneo and Java, Taiwan, the Japanese archipelago and Sakhalin, but not Madagascar. Most of the islands are continental in origin or close to other areas occupied by lacertids, suggesting that these lizards are not particularly good transmarine dispersers (compared with, for instance, geckoes and skinks). Body size is usually small, in most cases less than 120mm from snout to vent and down to

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* This was Boulenger's last task in a long and highly productive career. Even before the second volume of the monograph left the press, he quit the field, retired from the British Museum and returned to his native Belgium where he devoted his last years to studying roses. Anyone who has spent much time wandering in the confusing labyrinths of lacertid systematics will tend to sympathise.

33mm in *Ophisops beddomii*, but a couple of species sometimes reach 210mm and a Pleistocene form in the Canaries attained an estimated total length of 1200mm (Bravo, 1953). The majority of forms are ground-dwelling in a range of open and partly closed habitats, but a number climb on rock faces and among vegetation. Lacertids occur from tundra and high mountain habitats through heath, scrub and Mediterranean associations to tropical forest, semi-desert and desert. All species are essentially diurnal and all that have been checked appear to be heliotherms, even ones confined to rain forest. Most lacertids feed mainly on arthropods but some species of *Gallotia* are almost entirely vegetarian, at least when adult. The majority of lacertids appear to be active hunters but some use a sit-and-wait strategy to a considerable extent, for instance *Meroles suborbitalis* and *Pedioplanis lineoocellata* (Pianka, Huey and Lawlor, 1979). All, except most *Lacerta vivipara* and three species of *Eremias*, lay eggs (1 – 25 per clutch), the exceptions bearing fully formed young. In many respects, the Lacertidae are a conservative family including no forms with reduced limbs, eyes or ears, no nocturnal or aquatic species and few food specialists; nor do they have distinctive complex morphological adaptations, like the adhesive pads of geckoes, or the specialised tongues of chameleons.

DISTINCTIVE FEATURES OF THE LACERTIDAE

Snout narrow, premaxilla single, nasals paired, maxilla usually contacting frontal dorsally and separating nasal from prefrontal, frontals paired or fused in adults, parietal bone single with anterior tabs but without lateral downgrowths, supratemporal processes of parietal long and parietal table may extend backwards, pineal fontanelle present in most cases, fronto-parietal suture usually showing at least some interdigitation, postorbital and postfrontal bones separate or fused, the latter roofing the supratemporal fossa, supratemporal bone present; lachrymal present, forming lower border of orbit with jugal which may have a quadratojugal process; vomers paired, pyriform recess (interpterygoid vacuity) narrow; pterygoid teeth present or absent; alar process long to very reduced, posterior opening of vidian canal at basisphenoid-prootic suture; cranial osteoderms present and fused with skull bones when in contact with them, palpebral ossifications usually extensive. All mandibular elements present and Meckel's groove open, coronoid overlapping dentary labially; teeth pleurodont, usually bicuspid laterally, occasionally with more cusps. Nearly always 14 scleral ossicles in each eye; hyoid apparatus with ceratohyal and first and second ceratobranchial cartilages.

Presacral vertebrae vary from 22 to 33, females having a higher average number than males in nearly all species; usually three short and two long pairs of nuchal ribs; typically three pairs of ribs attaching to the sternum and two to the xiphisternum; last presacral vertebra sometimes lacking ribs. Clavicle usually expanded medially and perforated to form a continuous or posteriorly interrupted loop, interclavicle cruciform, sternum with a fontanelle in most cases, usually 0, 1 or 2 pairs of inscriptional ribs, rarely 3. Proximal autotomic caudal vertebrae with either one or two pairs of transverse processes, if two then posterior pair may be short and parallel to anterior one or long and diverging posteriorly.

Limbs unreduced, tail cylindrical; head covered by large symmetrical plate-like scales (Fig. 12), a collar (transverse posteriorly directed skin-fold on underside of neck covered externally by large scales) often present, belly scales large, femoral pores usual. Ulnar nerve superficial ('lacertide') or deep ('varanide'), dorsal muscles of the lower hind leg innervated by peroneal nerve (Julien & Renous-Lécuru, 1972). Jaw muscles characterised by a bodenaponeurosis divided into two lobes caudally and a parasaggital vertical sheet connecting the quadrate apneurosis to the temporal fascia (fide Rieppel, 1980). Cloacal muscles usually with a well defined posterior section of the m. transversus perinei (Arnold, 1984). Tongue quite deeply notched. Abdominal fat body often largely outside peritoneum; either lobes of hemipenis completely invested by m. retractor penis magnus, or lobes complexly folded and a complex hemipenial supporting structure, the armature, usually present.

Of these features, the lack of parietal downgrowths, usual presence of sexual variation in number of presacral vertebrae, fat-body position, hemipenial characteristics and perhaps the jaw muscle characters are largely or wholly restricted to the Lacertidae, at least among the Scincomorpha. Within the Lacertoidea, lacertids are further distinguished by closure of the temporal fenestra by the postfrontal.

RELATIONSHIPS OF THE LACERTIDAE

Camp (1923) placed the Lacertidae in the Lacertoidea within the Scincomorpha, along with the Teiidae sensu lato and the Gerrhosauridae (= subfamily Gerrhosaurinae of the Cordylidae). Relationship between the Lacertidae and Teiidae sensu lato has long been suggested (Underwood, 1971), for instance by Boulenger (1920) and has recently been argued by Estes, De Queiroz & Gauthier (1988), who treat these assemblages as sister groups which are successively related to the Xantusiidae, forming the Lacertoidea, and to the Scincoidea (Scincidae plus Cordylidae) to make up the Scincomorpha. Maclean (1974) divided Teiidae, as generally understood, into the subfamilies Teiinae, for the macroteiids, and Gymnophthalminae, for the microteiids. Subsequently, Estes (1983*a*) raised the latter group to family level, as did Presch (1983). Presch suggested it was the sister group of the Lacertidae but, as shown by Harris (1985), there is no evidence for this relationship in the form of synapomorphies.

Possible synapomorphies of Lacertidae and Teiidae plus Gymnophthalmidae (mainly from Estes, De Queiroz & Gauthier, 1988) are narrow snout and pyriform recess, interdigitating frontoparietal suture usually between prominent parietal tabs, adductor fossa widely open, heterodont dentition, often some caudal vertebrae with two pairs of transverse processes, tongue quite deeply notched, m. transversus perinei frequently with a differentiated posterior section.

TAXONOMIC UNITS USED IN ANALYSIS

Because a total phylogenetic analysis of over 230 species would be difficult, most have been combined into working units that are likely to be holophyletic (i.e. containing all the descendant species of a single ancestral one). In many cases, these units are recognized genera, but genera may be grouped or divided if there are reasons for believing they are not necessarily holophyletic as they stand. Ideally, holophyly is assumed because the members of the group concerned possess one or more unique derived characters (synapomorphies). In fact, holophyly sometimes has to be inferred from a combination of other indicators, such as close overall resemblance or serial resemblance among species, possession of a distinctive combination of derived features that, while not individually unique, are uncommon elsewhere, and a continuous geographical range. These indicators may also give additional support to holophyletic groups discerned on the basis of apparent synapomorphies.

In the following account, the number of recognised species in a taxonomic unit is given in parentheses and these are then listed. They are followed by any features that are unique to the group or nearly so, its geographical range, and references to any recent taxonomic studies that may be relevant. Hemipenial features mentioned are explained elsewhere (Arnold, 1986*a*).

Acanthodactylus (28): *arabicus, aureus, blanfordii, boskianus, boueti, cantoris, erythrurus, felicis, gongrorhynchatus, grandis, guineenisis, haasi, hardyi, longipes, maculatus, masirae, opheodurus, orientalis, pardalis, robustus, savignyi, schmidti, schreiberi, scutellatus, spinicauda, tilburyi, tristrami, yemenensis.*
First upper labial scale broad above but with sides converging downwards (Fig. 13c).
Range: Saharo-Sindian region, from Spain and North Africa through Middle East to Northwest India.
Salvador (1982); Arnold (1983).

Adolfus africanus etc (2): *africanus, vauereselli.*
Only four complete longitudinal rows of ventral scales.
Range: Equatorial Africa from Cameroon to Uganda, eastern Zaire and western Tanzania.
Arnold (1989).

Adolfus alleni
Range: mountains of Uganda and west Kenya above 2700m.
Arnold (1989).

Algyroides (4): *fitzingeri, marchi, moreoticus, nigropunctatus.*
Lips on hemipenis very small.
Range: Southern Europe.
Arnold (1973); Böhme (1981).

Aporosaura: see *Meroles-Aporosaura.*

Bedriagaia (1): *tropidopholis*
Range: Eastern Zaire
Arnold (1989).

Cabrita: see *Ophisops-Cabrita.*

Eremias (23): *acutirostris, andersoni, argus, arguta, aria, brenchleyi, buechneri, fasciata, grammica, intermedia, lineolata, multiocellata, nigrocellata, nikolskii, persica, pleskei, przewalskii, quadrifrons, regeli, scripta, strauchi, velox, vermiculata.*
Rostral scale narrowed with sides sloping inwards and downwards towards mid-line (also present in *Meroles reticulatus*).
Range: Palaearctic region, from eastern Europe and Turkey to China and adjoining USSR and south into Iran and Pakistan.
Shcherbak (1974).

Gallotia (4): *atlantica, galloti, simonyi, stehlini.*
Forty chromosomes (Cano, Baez, Lopez-Jurado & Ortega, 1984); no sexual variation in number of presacral vertebrae (approached by a few species of *Acanthodactylus*); dark chevrons frequent on throat.
Range: Canary Islands.
Böhme & Hutterer (1985).

Gastropholis (2): *prasina, vittata.*
Range: Coastal Kenya, Tanzania and Mozambique.
Arnold (1989).

Heliobolus (5): *lugubris, neumanni, nitida, quadrinasalis, spekii.*
Range: Africa south of the Sahara desert.

Holaspis (1): *guentheri*
Maxilla not contacting frontal dorsally, only 12 scleral ossicles in each eye, extra fontanelle in scapulocoracoid; frontoparietal scales fused to each other and to interparietal, lateral dorsal body scaling transversely expandable, tail depressed with lateral fringes of pointed scales.
Range: Equatorial Africa from Sierra Leone south to Angola and thence eastwards to Tanzania, Mozambique and Malawi.
Arnold (1989).

Ichnotropis (7): *bivittata, capensis, chapini, grandiceps, microlepidota, squamulosa, tangicana.*
Coarse plication on basal parts of hemipenial lobes.
Range: Southern Africa north to Congo, Zaire and Tanzania.

Lacerta agilis group (7): *agilis, media, pamphylica, schreiberi, strigata, trilineata, viridis*
Range: Europe, central and southwestern Asia.
Peters (1962*a*), Arnold (1973), Böhme (1984), Schmidtler (1986).

Lacerta andreanszkyi
Range: Atlas of Morocco.

Lacerta – archaeolacertas etc (23): *armeniaca, bedriagae, caucasica, clarkorum, chlorogaster, dahli, defilippi, derjugini, horvathi, lantzicyreni, mixta, monticola, mosorensis, parvula, portschinskii, praticola, raddei, rostombekovi, rudis, saxicola, unisexualis, uzzelli, valentini.*
Range: Southern Europe, Caucasus and neighbouring Southwest Asia.
Darevskii (1967); Bannikov, Darevskii, Ischenko, Rustamov & Shcherbak (1977); Böhme (1984).

'Lacerta' australis etc (2): *australis, rupicola.*
Range: South Africa (Western Cape Province and northern Transvaal).
FitzSimons (1943).

Lacerta brandtii
Range: Northwest Iran and adjoining USSR.

Lacerta cappadocica
Range: East Turkey, North Iraq, Northwest Iran.
Eiselt (1979).

Lacerta danfordi etc. (3): *anatolica, danfordi, oertzeni.*
Range: Southwest Turkey and offshore islands.
Eiselt & Schmidtler (1987).

Lacerta dugesii
Range: Madeira.
Richter in Böhme (1986).

'Lacerta' echinata
Range: Equatorial Africa from Liberia to eastern Zaire.
Arnold (1989)

Lacerta graeca
Range: Southern Greece.

'Lacerta' jacksoni
Range: mountains of eastern Zaire, Uganda, Kenya and Tanzania.
Arnold (1989).

Lacerta jayakari etc (2): *cyanura, jayakari.*
Range: Oman, southeastern Arabia.
Arnold (1972, 1973); Lutz, Bischoff and Mayer (1986).

Lacerta laevis
Range: Southeast Turkey, Syria, Lebanon, Israel, Jordan, Cyprus.

Lacerta lepida etc (2): *lepida, pater.*
Range: Southwest Europe, Northwest Africa.
Bischoff (1982).

Lacerta oxycephala
Range: Southwest Yugoslavia.

Lacerta parva etc (2): *fraasii, parva.*
Lobes of hemipenis not plicate, but with longitudinal flaps.
Range: Turkey and adjoining USSR; Lebanon.
Peters (1962*b*); Arnold (1973).

Lacerta perspicillata
Range: Northwest Africa.
Richter in Böhme (1986).

Lacerta princeps
Range: Southeast Turkey to West Iran.
Eiselt (1968, 1969).

Lacerta vivipara.
Range: Europe eastwards across northern Asia to Sakhalin island.

Latastia (8): *boscai, carinata, cherchii, doriai, johnstonii, lanzai, longicaudata, taylori.*
Range: Southwest Arabia, Nigeria to Sudan, Somalia, Kenya, Tanzania, Mozambique, Malawi, eastern Zaire, Zambia, Zimbabwe.
Arillo, Balletto & Spanò (1967).

Meroles-Aporosaura (7).
Meroles (6): *ctenodactylus, cuneirostris, knoxii, micropholidotus, reticulatus, suborbitalis*
Aporosaura (1): *anchietae*
Hemipenial clavulae conjoined at base (not checkable in highly modified hemipenis of *M. suborbitalis*). *Aporosaura* shares many features with advanced *Meroles*.
Range: Coastal Angola, Namibia and western South Africa.
Arnold (in press).

Mesalina (11). *adramitana, ayunensis, balfouri, brevirostris, guttulata, martini, olivieri, pasteuri, rubropunctata, simoni, watsonana.*
Clavulae directly attached to hemipenial lobes.
Range: Saharo-Sindian region from North Africa, through Middle East to Northwest India.
Arnold (1986*a*, 1986 *b*).

Nucras (7): *boulengeri, caesicaudata, intertexta, lalandii, scalaris, taeniolata, tessellata.*
Exposure of ectopterygoid bone on the side of the skull below maxilla very marked; first three pairs of nuchal ribs with cylindrical terminal cartilages.
Range: Southern Africa north to Kenya, Uganda and Angola.
Broadley (1972).

Ophisops-Cabrita (8)
Ophisops (6): *beddomii, elbaensis, elegans, jerdoni, microlepis, occidentalis*
Cabrita (2): *jerdonii, leschenaultii.*
Huge undivided window in lower eyelid.
Range: North Africa, Southwest Asia, Indian subcontinent.
Arnold (in preparation)

Pedioplanis (11): *benguelensis, breviceps, burchelli, gaerdesi, inornata, laticeps, lineoocellata, husabensis, namaquensis, rubens, undata.*
Outer connectors arise very close together on dorsum of hemipenial armature and may fuse (not always apparent in forms with highly modified hemipenes).
Range: Southern Africa north to Angola and Transvaal.
Arnold (in press).

Philochortus (6). *hardeggeri, intermedius, lhotei, neumanni, phillipsi, spinalis.*
Distinctive hemipenial pattern with peculiar outer connectors; long and short dorsal ribs poorly differentiated.
Range: Southwest Arabia, Somalia, Ethiopia, northern Kenya; scattered relict populations in North Africa.

Platyplacopus: see *Takydromus-Platyplacopus.*

Podarcis (15): *bocagei, erhardii, filfolensis, gaigiae, hispanica, lilfordi, melisellensis, milensis, muralis, peloponnesiaca, pityusensis, sicula, taurica, tiliguerta, wagleriana.*
Range: Central and southern Europe, Northwest Africa, Northwest Turkey.
Böhme (1986).

Poromera (1): *fordii.*
Hemipenis symmetrical but not bifurcate, with loosely folded walls in retracted organ.
Range: Cameroon, Rio Muni, Gabon, Congo [?].

Psammodromus algirus
Range: Southwest Europe, Northwest Africa.
Very strongly overlapping ventral scales.
Böhme (1981).

Psammodromus hispanicus etc. (3): *blanci, hispanicus, microdactylus.*
Femoral pores enlarged in inguinal region.
Range: Southwest Europe, Northwest Africa.

Pseuderemias (5). *brenneri, erythrosticta, mucronata, smithi, striata*
Four scales round nostril (also present in some *Ophisops*); very narrow snout (also present in *Meroles reticulatus* and *Acanthodactylus masirae*).
Range: Coastal Sudan, Ethiopia, Djibouti, Somalia, northern Kenya.

Takydromus-Platyplacopus (14)
Takydromus (10): *amurensis, haughtonianus, hsuehshanensis, khasiensis, sauteri, septentrionalis, sexlineatus, smaragdinus, tachydromoides, wolteri.*
Platyplacopus (4): *dorsalis, intermedius, kuehnei, sylvaticus*
Lateral teeth with three cusps (shared only with some *Gallotia*); femoral pores well developed but reduced to 1 to 3

on each side; lobes of retracted hemipenis with dorsoventrally compressed or triskelial transverse section.
Range: Japanese archipelago, Taiwan, Korea, adjoining USSR and China westwards to Assam and south to Borneo and Java.

Tropidosaura (4): *cottrelli, essexi, gularis, montana.*
Range: South Africa.
FitzSimons (1943).

Species not considered due to unavailability: *Lacerta mostoufii* Baloutch, (1977), *Eremias ercolinii* Lanza & Poggesi (1975).

DETERMINATION OF CHARACTER POLARITY

There are a number of methods for determining the polarity of characters, that is which state is likely to be primitive in the group under investigation and what its relationships to other states are. Some aspects of this process are discussed elsewhere (Arnold, 1981*a*) and the indicators used here explained below.

Outgroup analysis

If a character has two or more states within the studied group and one is also widespread in related taxa, that is in outgroups, it is likely to be primitive within the studied group. Sucessive principal outgroups of the Lacertidae among squamates appear to be Teiidae plus Gymnophthalmidae, Xantusidae, Scincidae + Cordylidae, Anguoidea, Gekkota and Iguania (Estes, De Queiroz & Gauthier, 1988), with the position of snakes and amphisbaenians not precisely determined. Further outgroups among the living tetrapods are *Sphenodon*, other amniotes and amphibians. A state found throughout all these groups is very probably primitive in the Lacertidae, but it is rare for cases to be so unequivocal. Often insufficient information exists about the distribution of states in the outgroups, or states are difficult to recognise with certainty in the more distant ones. Again, it is not uncommon for more than one state to occur in the outgroups, albeit often at different frequencies. Because of these problems, outgroup evidence of primitiveness has been divided into criteria of generally diminishing strength. 1. State widespread in tetrapods or at least lizards. 2. State universal or nearly so in scincomorphs other than lacertids (Teiidae, Gymnophthalmidae, Xantusidae, Scincidae and Gerrhosauridae). 3. State found in majority of scincomorphs other than lacertids. In general, distribution across a range of outgroups, even if the state concerned is absent from the most immediate one, is given more credence as an indicator of primitiveness than presence in the immediate outgroup alone. This is because the latter situation is likely to involve reversal which, in many characters, seems less probable than parallel development in the studied group and its immediate outgroup. 4. State present in primitive members of scincomorph families.

Even in cases where there is a strong and consistent indication of polarity in the outgroups, this method may not always correctly predict the primitive state in the group under consideration. This is especially likely if the character turns out to be very homoplastic in the studied group, so that it is clearly labile and more likely to have reversed in the ancestral stem.

Outgroup techniques within studied group

Outgroup techniques can be used within the studied group, if holophyletic subgroups can be established within it. Thus, if one state of a character is generally widespread and also occurs in a holophyletic subgroup (such as those listed in the previous section) with another state restricted to this, then the latter is likely to be derived. This technique is more powerful once a substantial part of the phylogenetic structure of the group is established. Outgroups can then often be determined for each subgroup concerned and polarity estimated with more certainty for that subgroup, even if the restricted state also occurs in others.

Ontogeny

Appearance first in development is often cited as an indication of primitiveness and quite frequently agrees with other polarity indicators, although conflicts are not uncommon.

Commonality

States that are widespread in the studied group are, on average, more likely to be primitive, although many exceptions to this generalisation are likely.

Presence in most primitive forms

By and large, states found in the most primitive members of a group are more likely to be primitive themselves. Initial analysis establishes an assemblage of primitive forms in the Palaearctic and Oriental regions (p. 230).

Compatibility analysis

The compatibility technique used here (p. 229), which does not involve any prior assumptions of polarity, produces a preferred set of compatible (non-conflicting) characters. Character state distribution within such a set may be represented by a bifurcating diagram joining the taxa (Fig. 1). If

	Taxa							
	A	B	C	D	E	F	G	H
Characters								
1	0	0	1	1	1	1	1	1
2	1	1	0	0	1	1	1	1
3	1	1	1	1	0	0	0	0
4	1	1	1	1	0	0	1	1
5	1	1	1	1	1	1	0	0
6	0	0	0	0	1	1	1	1

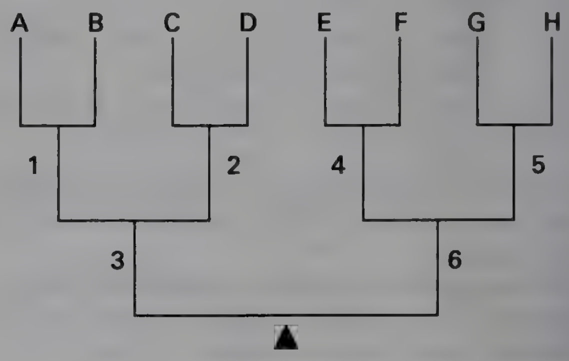


Fig. 1 Hypothetical set of compatible characters for taxa A to H, and a diagram based on the distributions of their states. Figures in diagram indicate where particular states of characters change. ▲ indicates where root subsequently established.

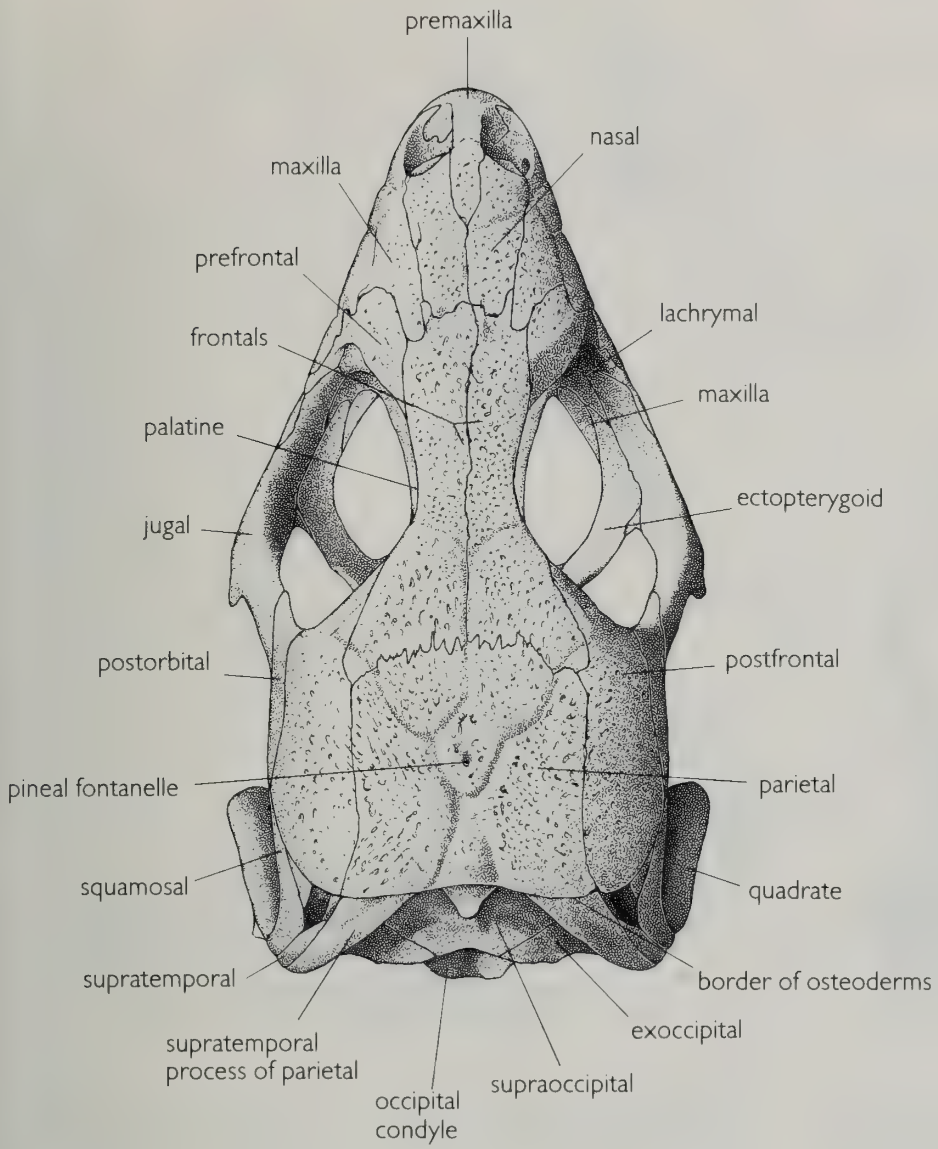


Fig. 2 Skull of primitive lacertid (*Podarcis taurica*), with thick osteodermal layer (crusta calcarea), showing principal dorsal bones.

the polarity of some of the characters is known from other sources, such as outgroup comparison, the diagram can be rooted and converted into a putative phylogeny. It may then be used to retrospectively determine the direction of change of characters of previously unknown polarity. For instance in Fig. 1, if it is known from other sources that the 1 states of characters 3 and 6 are derived, so that taxa A, B, C and D, and E, F, G and H, are likely to be distinct holophyletic groups, then it is clear that the 0 states of characters 1, 2, 4 and 5 are also likely to be derived. The root of the putative phylogeny can consequently be established. Direction of change in such a diagram can also sometimes be confirmed by the distribution of characters that are not in the original compatible set. For instance, if this set specifies an assemblage of taxa that is only part of the studied group, a secondary analysis confined to that assemblage will often produce a larger set of compatible characters for this assemblage, and some of the additional ones may be helpful in determining the direction of character change. Characters that fail to be included in compatible sets because of limited homoplasy can also sometimes be useful in this respect.

In lacertids, compatibility analysis produces a hierarchical pattern of character distribution associating *Lacerta jayakari* (Fig. 19) etc and Ethiopian and advanced Saharo-Eurasian lacertids, and another for *Psammodromus* and its relatives; characters of uncertain polarity in these areas can consequently be resolved, at least provisionally. In the former case, direction of change is confirmed by the following characters with good polarity indications from other sources: 3, 4, 5, 10, 27, 34, 63 and 81. In the *Psammodromus* series direction is determined by 18, 77, 82 and 83. It should be borne in mind that the *Psammodromus* tree is much less well supported than the one for Ethiopian and advanced Palaearctic lacertids, so polarities partly based on it must be treated with more caution.

The polarity indicators for each character are summarised in Appendix 1. In some cases polarity is discussed further in the section on characters used in analysis (p. 216).

Conflict of evidence

In most characters, the evidence for polarity is unequivocal, although its strength varies considerably. However, there are twelve in which there is some conflict between the sources of polarity evidence: 1, 7, 11, 22, 26, 28, 31, 32, 41, 43, 61 and 66. In character 1, ontogeny conflicts with a wide range of other evidence and can be discounted. In most of the others, outgroup evidence contradicts that from other sources, but in general the former is relatively weak, the presumed primitive state being found in the majority of other scincomorphs, rather than being the only condition in outgroups. Consequently, it seems appropriate to accept the evidence from other sources, at least initially. In characters 22, 28, 31, 32 and 43, outgroup evidence is generally stronger but again is

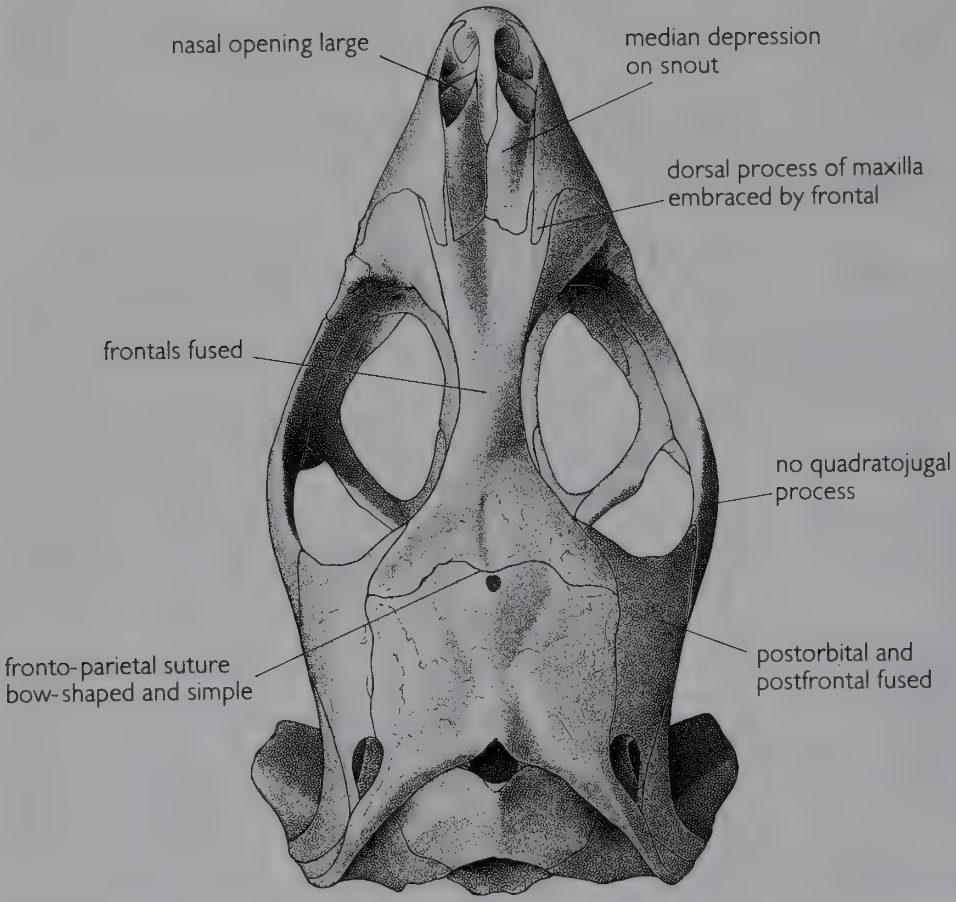

nasal opening large
median depression on snout
dorsal process of maxilla embraced by frontal
frontals fused
no quadratojugal process
fronto-parietal suture bow-shaped and simple
postorbital and postfrontal fused

Fig. 3 Skull of advanced lacertid (*Pedioplanis lineoocellata*), with thin osteodermal layer (crusta calcarea), showing common derived conditions. The cranial osteoderms terminate more anteriorly than in primitive forms.

contradicted by other sources which will be provisionally accepted, although conflict here is more severe. Because of this, the data set is also analysed with these particular polarities reversed (p. 231).

CHARACTERS USED IN ANALYSIS

Characters used in analysis are listed below and their distribution summarised in Appendix 2. Each primary character is numbered. Where these have more than two states they are divided into further binary characters, which are designated by figures after a decimal point. Each state of a binary character is indicated by 0 or 1, the former being attached to the apparent primitive condition of the character. Eighty-four primary characters are used, producing a total of 112 binary characters. Borders between some character states are of necessity rather arbitrary. References to fuller explanations of some characters are given, and hemipenial features are described elsewhere (Arnold, 1986*a*, 1973).

Skull

1 *Nasal opening of skull* (Figs 2,3). Small (0); large (1).

2.1, 2.2, 2.3, 2.4 *Septomaxilla* (Fig.4). Simply convex above with a rounded posterior margin and a narrow anterior shelf with at most slight anterior and posterior projections (0,0,0,0) – Fig. 4a; with distinct and widely separated anterior and posterior projections (1,0,0,0) – Fig. 4b; with distinct and widely separated anterior and posterior projections and a clear posterolateral process (1,1,0,0) – Fig. 4c; with distinct posterior projection and posterolateral process but no anterior projection (1,1,1,0) – Fig. 4d; with distinct posterior projection and posterolateral process, no anterior projection but an anterolateral process (1,1,1,1) – Fig. 4e, f.

3.1, 3.2 *Medial depression on snout* (Figs 2,3). Absent (0,0); weak (1,0); strong (1,1).

4 *Frontal bones* (Figs 2,3). Separate throughout life (0); fused, at least in mature animals (1).

5 *Dorsal process of maxilla* (Figs 2,3) Broad, at most only slightly embraced by processes of frontal bone (0); narrower and often quite extensively embraced by narrow processes of frontal bone (1).

6.1, 6.2 *Anterior descending processes of frontal bone.* Reaching palatines and in continuous contact with prefrontal, so anterior surface of orbit is completely bony (0,0); not descending fully or a window present between each process and the adjoining prefrontal bone (1,0); processes absent (1,1).

7 *Fronto-parietal suture* (Figs 2,3). Convex anteriorly, the median section interdigitating strongly with the frontal (0); typically bow-shaped with a small concavity near midline, only quite weakly interdigitating with the frontal or scarcely at all (1).

8 *Length of parietal bone/length of section bearing osteoderms or at least covered by large dermal plates*. Less than 1.45 (0); more than 1.45 (1).

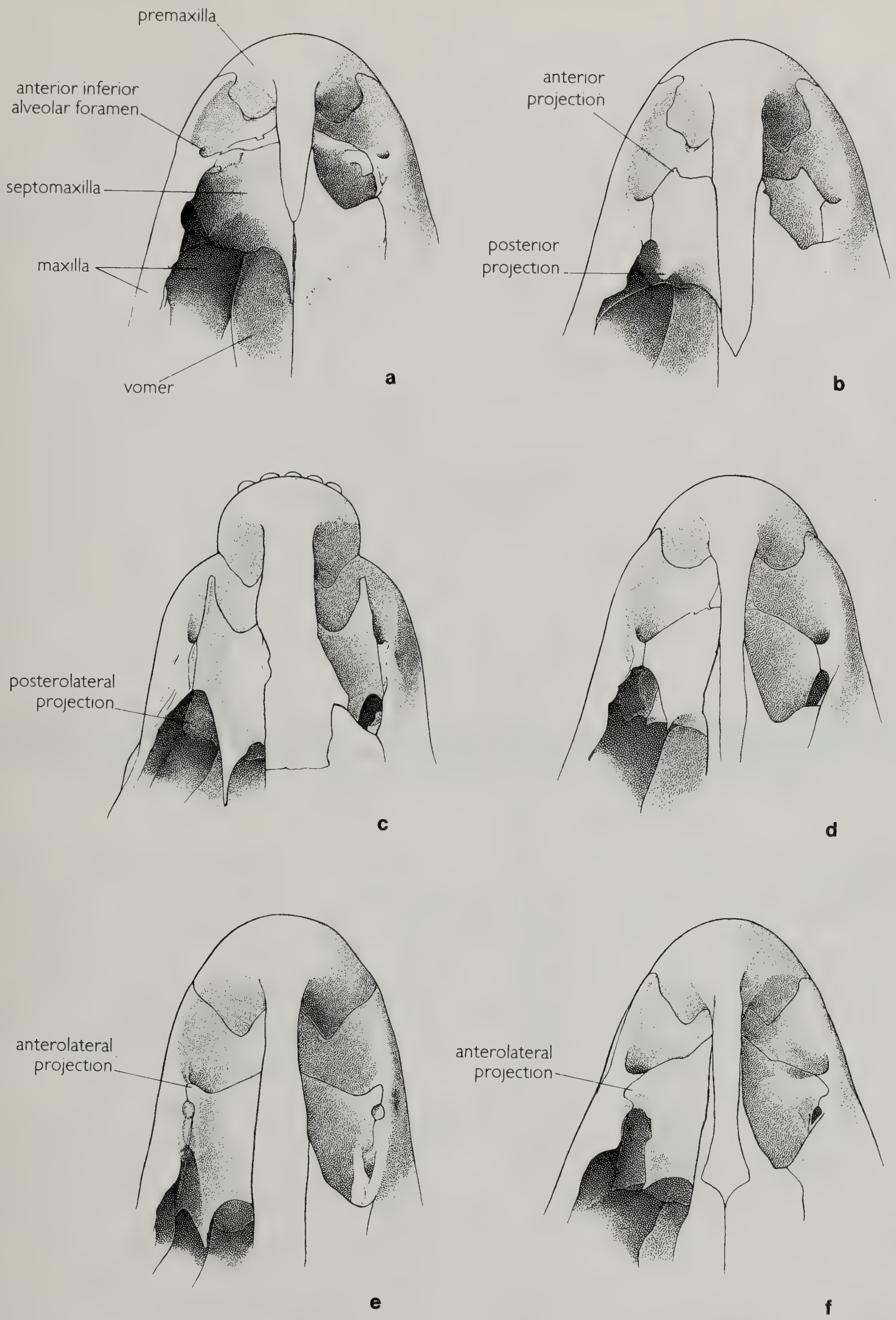

premaxilla
anterior inferior alveolar foramen
septomaxilla
maxilla
vomer
a
anterior projection
posterior projection
b
posterolateral projection
c
d
anterolateral projection
e
anterolateral projection
f

Fig. 4 Snouts of lacertid skulls with the left nasal cavity opened to show variation in the septomaxilla. a. *'Lacerta' jacksoni*; b. *Gallotia atlantica*; c. *Acanthodactylus schmidti*; d. *Pedioplanis laticeps*; e. *Mesalina balfouri*; f. *Ophisops elegans*.

9 *Width of parietal bone/length of section bearing osteoderms or at least covered by large dermal plates*. Less than 1.05 (0); more than 1.05 (1).

10.1, 10.2. *Pineal fontanelle* (Figs 2,3). Present (0,0); absent in many but not all individuals, or reduced (1,0); absent in all cases (1,1).

11 *Cranial osteoderms* (Figs 2,3). Reaching the back of the parietal bone extensively in medial area (0); not extending this far posteriorly or only over a small area (1).

12 *Postfrontal and postorbital bones* (Figs 2,3). Separate in adults, with rare exceptions (0); fused in adults and most young animals (1).

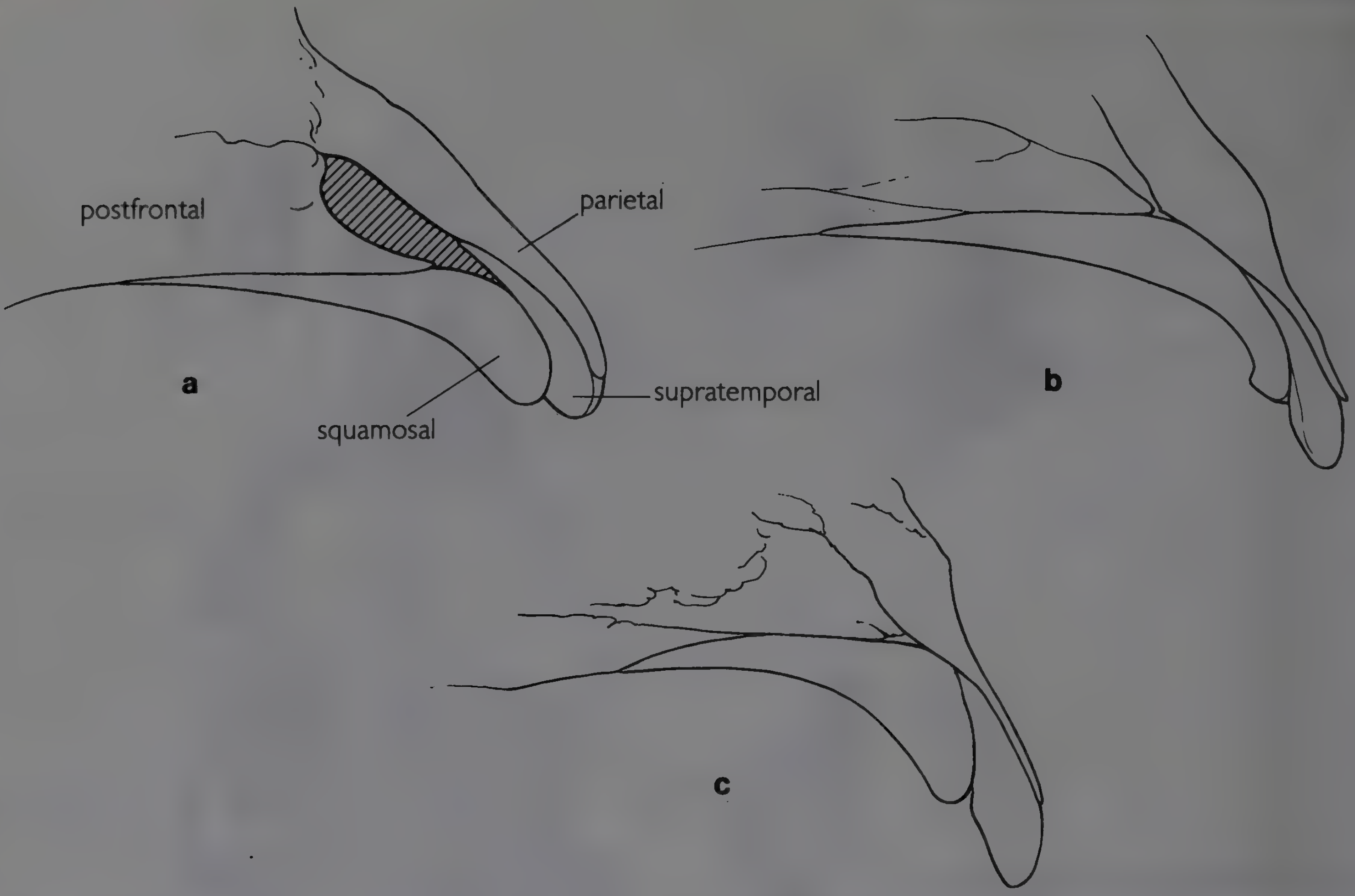

postfrontal
parietal
a
squamosal
supratemporal
b
c

Fig. 5 Posterolateral aspects of lacertid skulls (anterior to left), showing variation in shape of squamosal bone and its relationship to the supratemporal process of the parietal bone. a. fairly slender, separated from parietal (*Eremias arguta*); b. slender, in contact with parietal (*Nucras taeniolata*); c. deep posteriorly, in contact with parietal (*Pedioplanis lineoocellata*).

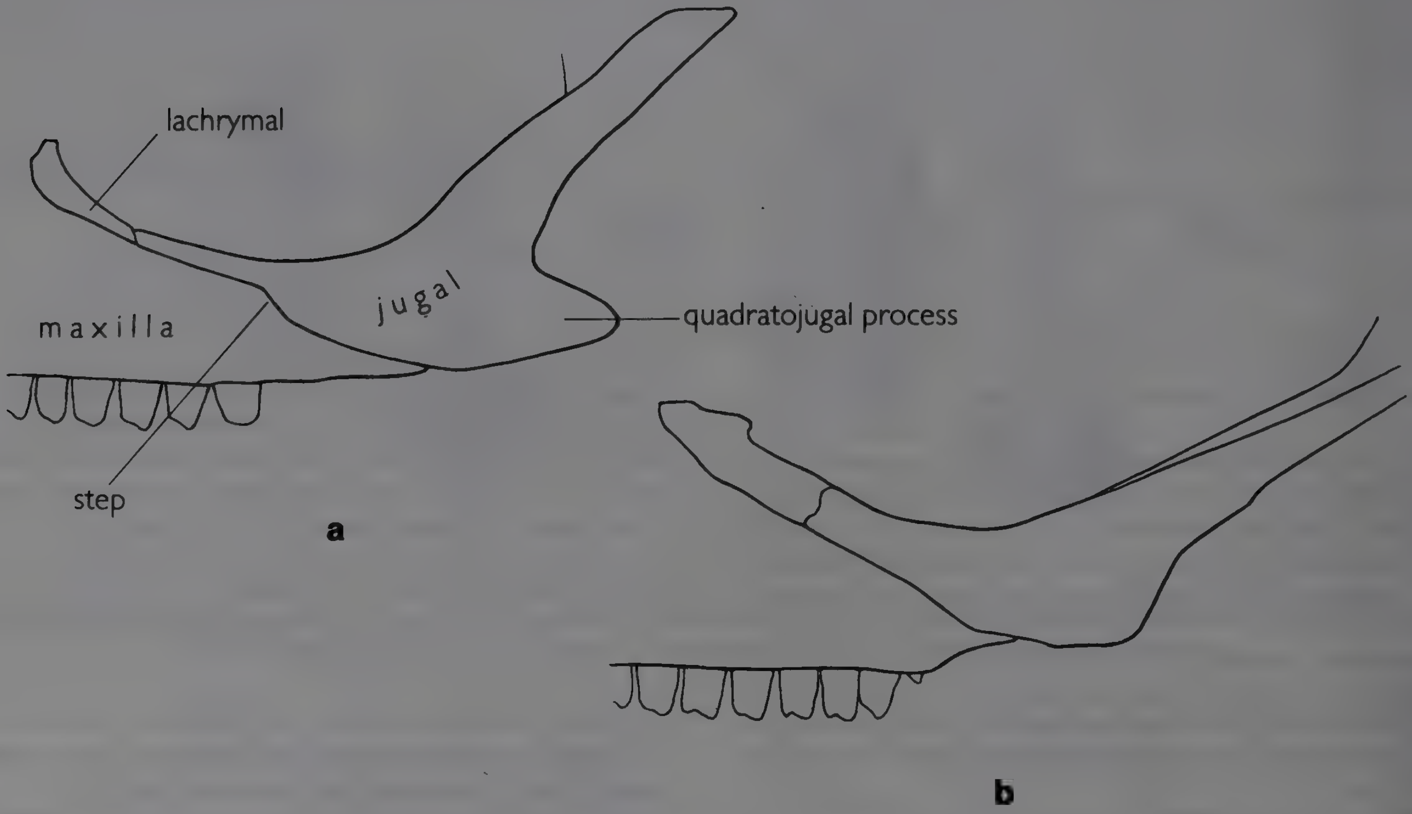

lachrymal
maxilla
jugal
quadratojugal process
step
a
b

Fig. 6 Suborbital area of lacertid skulls in lateral view, showing presence or absence of quadratojugal process on jugal bone, variation in extent of anterior jugal exposure, and presence or absence of a 'step' in the lower border of the jugal.

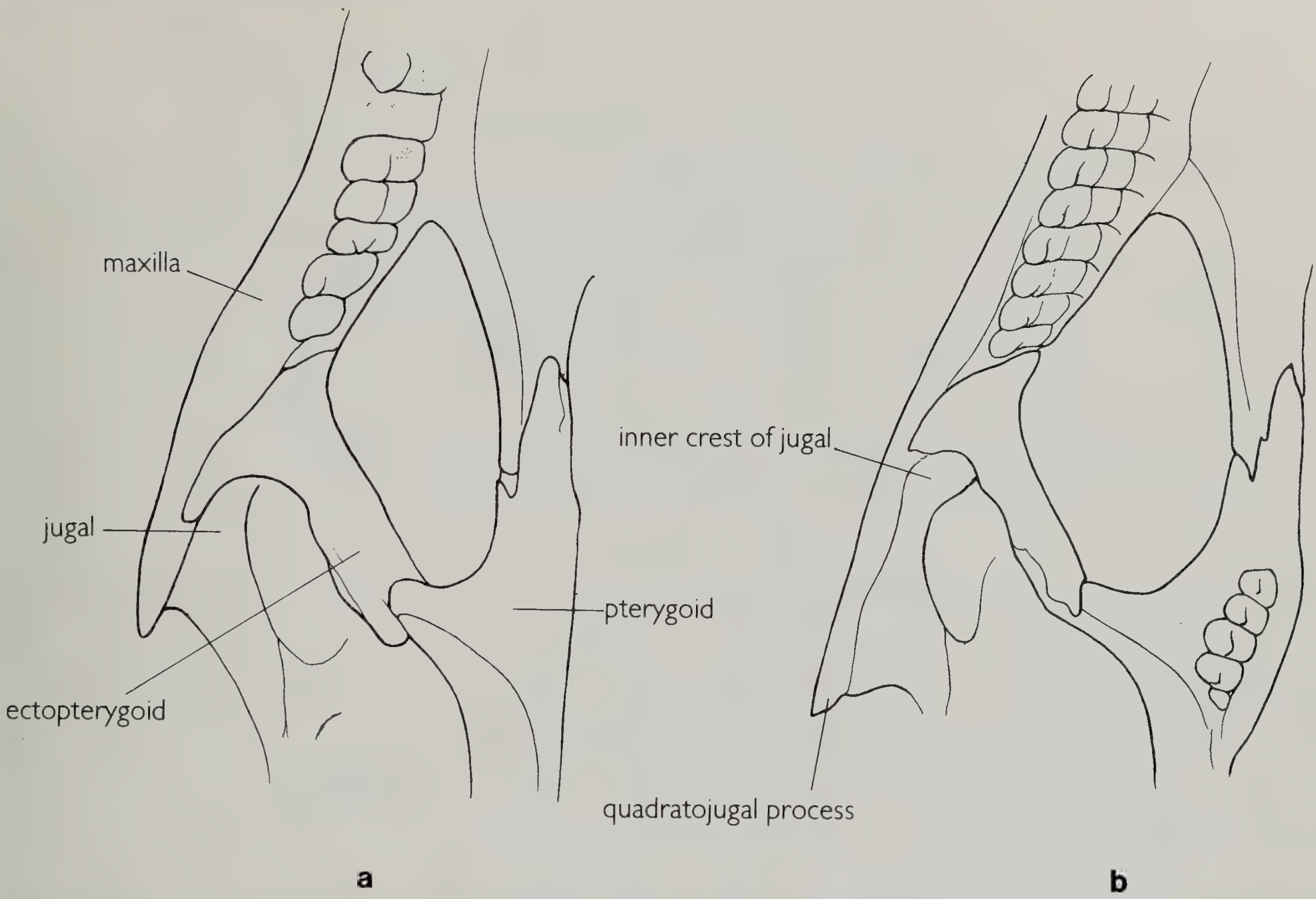


Fig. 7 Right suborbital region of lacertid skulls in ventral view. a. *Podarcis sicula*; b. *Psammodromus algirus* with inner crest of jugal bone clearly visible behind ectopterygoid.

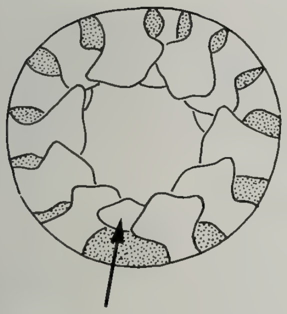


Fig. 8 Scleral ossicles of *Acanthodactylus*; arrow indicates scleral ossicle 14 which lacks a peripheral radial portion. From Arnold (1983).

13 *Contact between squamosal and parietal bones* (Fig. 5). Absent (0); present (1).

14 *Shape of squamosal bone* (Fig. 5). Slender (0); deep posteriorly (pistol shaped) (1).

15 *Quadratojugal process on jugal bone* (Fig. 6). Distinct (0); usually very reduced or absent (1).

16 *Exposure of anterior part of jugal bone on side of skull* (Fig. 6). Small (0); large (1).

17 *Lower border of outer face of jugal bone* (Fig. 6). Not markedly stepped (0); often markedly stepped (1).

18 *Inner crest of jugal bone clearly visible behind ectopterygoid in ventral view* (Fig. 7). No (0); yes (1).

19 *Ossification of temporal scales*. Not extensive (0); extensive (1).

20 *Lateral teeth*. With two cusps or sometimes one (0); usually with three or more cusps (1).

21 *Peripheral radial portion of scleral ossicle 14* (Fig. 8). Present (0); absent (1).

Post-cranial skeleton

22.1, 22.2 *Clavicle* (Fig. 9). Variable within species, medial part loop-shaped, either continuous or interrupted posteriorly (0,0); always interrupted posteriorly (1,0); never interrupted posteriorly (0,1).

23 *Expansion of medial section of clavicle* (Fig. 9). Strong (0); weak (1).

24 *Shape of interclavicle* (Fig. 10). Cruciform, with arms directed laterally, or obliquely forwards (0); arms directed obliquely backwards (1).

25 *Interclavicle flanged*. No (0); yes (1).

26.1, 26.2, 26.3 *Sternal fontanelle* (Fig. 10). Large and roughly elliptical (0,0,0); sometimes very weakly heart-shaped (1,0,0); clearly heart-shaped in at least some individuals (1,1,0); small and round, or absent (0,0,1).

27 *Xiphisternal cartilages* (Fig. 10). Close together or in contact (0); well separated (1).

28 *Marked sexual variation in number of presacral vertebrae*. Yes (0); no (1).

Outgroup analysis among the Scincomorpha suggests that marked sexual variation is likely to be the derived condition in lacertids. But the alternative state (little or no sexual variation) has a very restricted distribution in the Lacertidae. It occurs in a few species of *Acanthodactylus*, where outgroup comparison within Ethiopian and advanced Saharo-Eurasian genera indicates it is secondary, and also in *Gallotia*, where outgroup comparison among related primitive forms suggests the same thing.

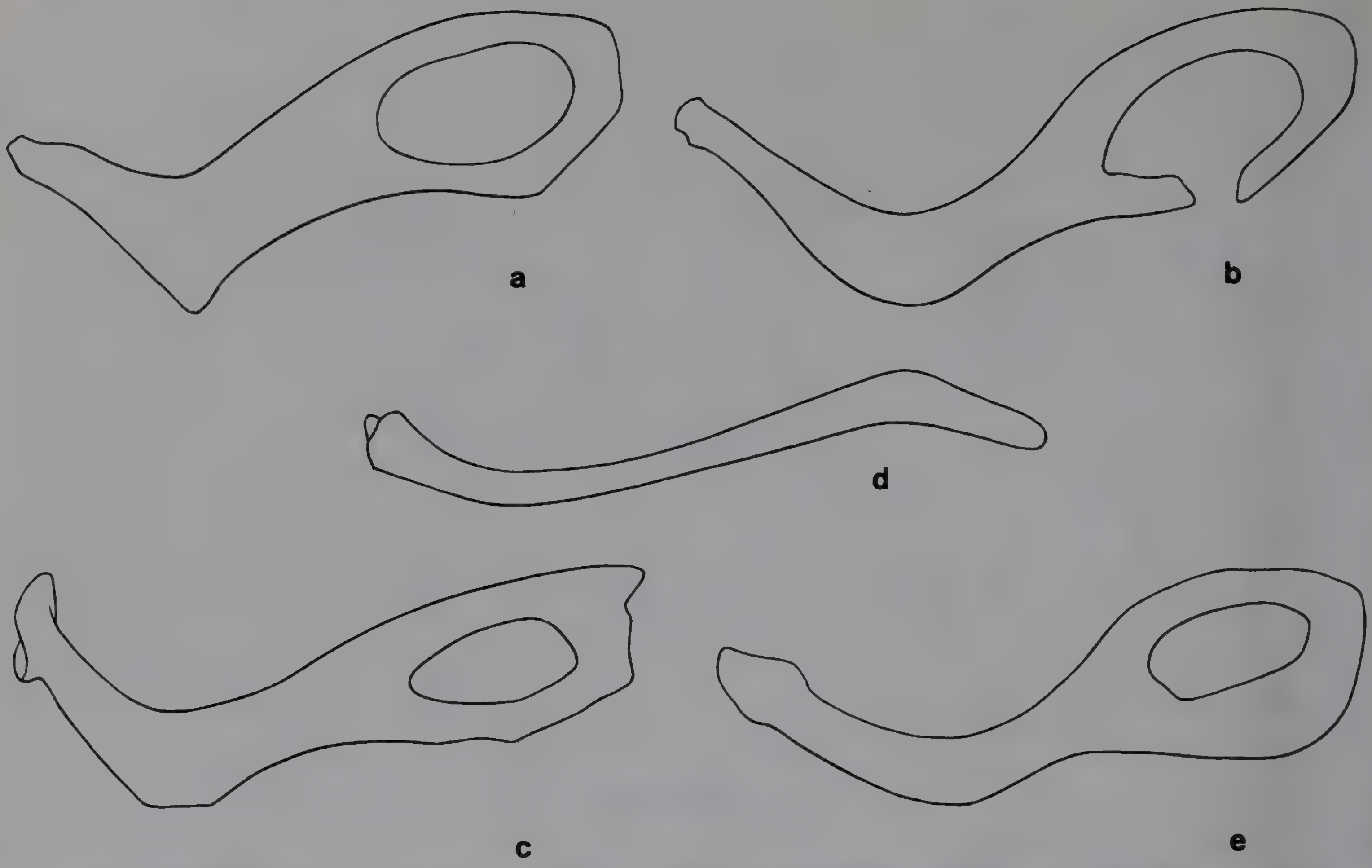


Fig. 9 Right clavicles in ventral view, showing variation in medial area. a. strongly expanded, forming continuous loop (*Lacerta* s. str).; b. strongly expanded, loop interrupted posteriorly (*Lacerta* s. str.); c. weakly expanded, forming continuous loop ('*Lacerta' echinata*); d. posterior section completely absent (*Holaspis guentheri*); e. weakly expanded, forming continuous loop with posterior border thickened (*Adolfus vaueresellі*).

29 *Number of short free dorsal ribs*. Equal or less than number of long free dorsal ribs (0); More than number of long free dorsal ribs (1).

30 *Inscriptional ribs*. Often present (0); often absent (1).

31.1, 31.2, 31.3 *Transverse processes on anterior automatic caudal vertebrae* (Fig. 11). Variable within species, in some individuals a long anterior pair of processes more or less at right angles to the vertebra and a shorter parallel posterior pair—pattern B, others lack the posterior pair—pattern A (0,0,0); only anterior pair present in all individuals—pattern A (1,0,0); a long anterior pair and a posterior pair that diverges posteriorly and may sometimes be rather longer—pattern BC (0,1,0); posterior pair diverging posteriorly and always longer than anterior one—pattern C (0,1,1).

Etheridge (1967) considered pattern C as the primitive one in lacertids, but it and pattern A are both widespread in lizards as a whole and, if anything, the assumption that pattern A is derived is more parsimonious overall. Among advanced lacertids, the distribution of other characters in compatibility analysis suggests that the C pattern in *Acanthodactylus*, *Mesalina* and *Ophisops-Cabrita* arose directly or indirectly from pattern A (p. 230). An indication that such a change is possible is provided by a specimen of *Pedioplanis lineoocellata* (BMNH 98.5.4.3) in which one side of the tail shows the A pattern, like other members of *Pedioplanis*, while the other exhibits a close approximation to the C condition. Distribution of other characters also indicates that the C pattern is likely to be derived from the BC pattern in *Psammodromus* and *Gallotia* (p. 232) and from the A/B polymorphism in *Podarcis* (p. 234). Compatibility analysis associating *Lacerta jayakari* with Ethiopian and advanced Saharan and Eurasian lacertids, and commonality within primitive lacertids both suggest that the A/B polymorphism is likely to be primitive.

External features of head (Fig. 12)

32 *Postnasal scales*. Two superposed (0); single (1).

33 *Contact between postnasal and supranasal scales below level of nostril*. Absent (0); present (1).

34 *Lower postnasal scale extending anteriorly to contact rostral scale* (Fig. 13). No (0); yes (1).

35 *Contact between supranasal and anterior loreal above single postnasal*. Absent (0); present (1).

36 *Extended lower postnasal divided*. No (0); yes (1).

37 *Width of rostral scale*. Normal (0); narrow with sides sloping inwards towards mid-line (1).

38 *Second supraciliary scale elongate, extending posterior to suture between second and third supraoculars*. No (0); yes (1).

39.1, 39.2 *Position of lateral border of parietal scale relative to parietal table of skull* (Fig. 14). Not reaching edge of table (0,0); reaching edge of table posteriorly (1,0); reaching edge of table anteriorly as well (1,1).

40.1, 40.2 *Size of occipital scale*. Normal (0,0); broad, as wide as posterior border of frontal in adults (1,0); strongly reduced or absent (0,1).

41.1, 41.2 *Interparietal scale* Normal (0,0); often enlarged (1,0); absent or extremely reduced (0,1).

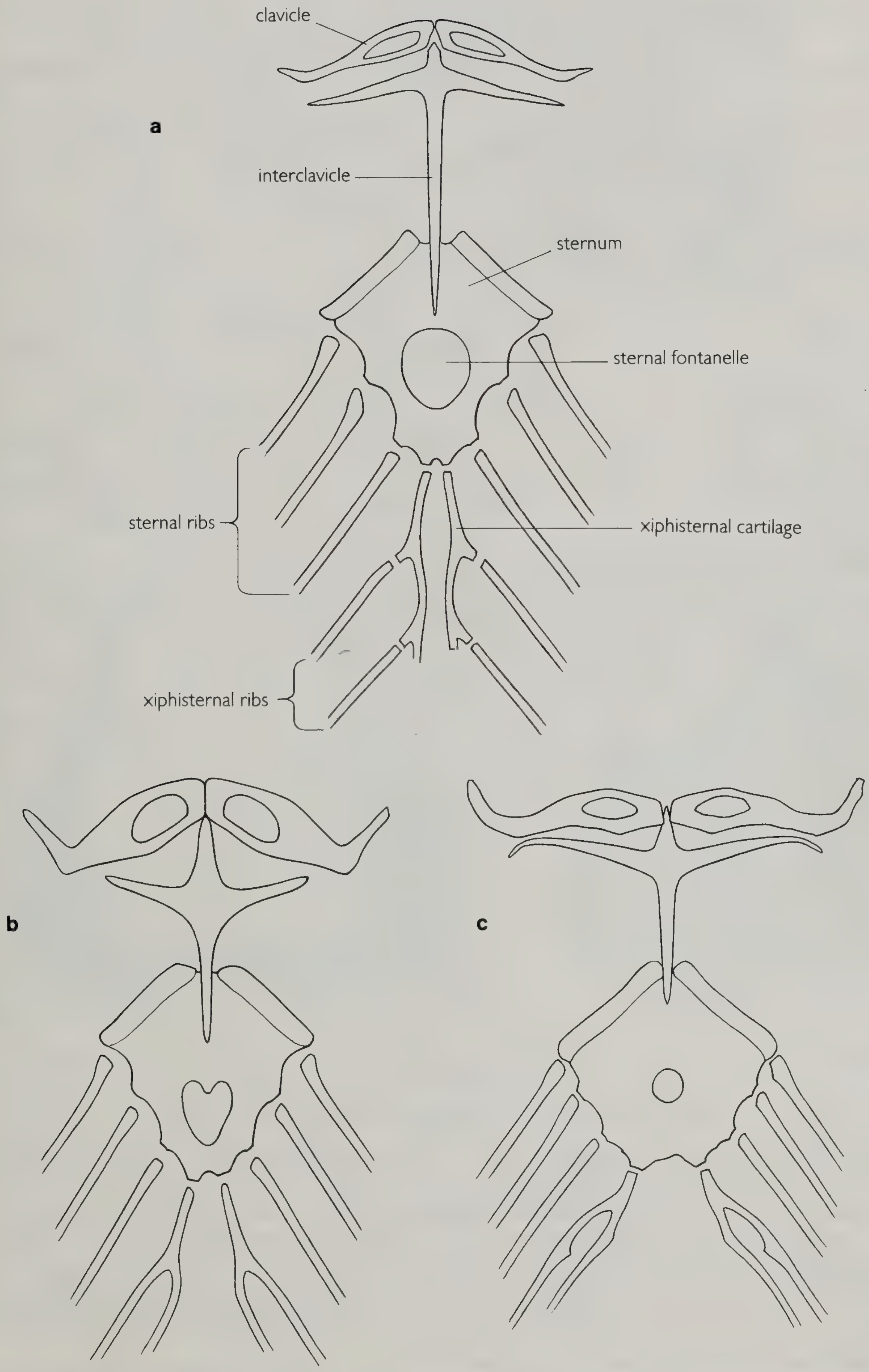

clavicle
a
interclavicle
sternum
sternal fontanelle
sternal ribs
xiphisternal cartilage
xiphisternal ribs
b
c

Fig. 10 Clavicles, interclavicles, sterna and associated ribs and cartilages, showing variation. a. Interclavicle with arms directed obliquely backwards, sternal fontanelle large and elliptical, xiphisternal cartilages close together (*Lacerta dugesii*); b. interclavicle with arms directed obliquely forwards, sternal fontanelle heart-shaped, xiphisternal cartilages distinctly separated (*Acanthodactylus boskianus*); c. interclavicle with arms directed obliquely forwards, sternal fontanelle small and round, xiphisternal cartilages broadly separated (*Meroles ctenodactylus*).

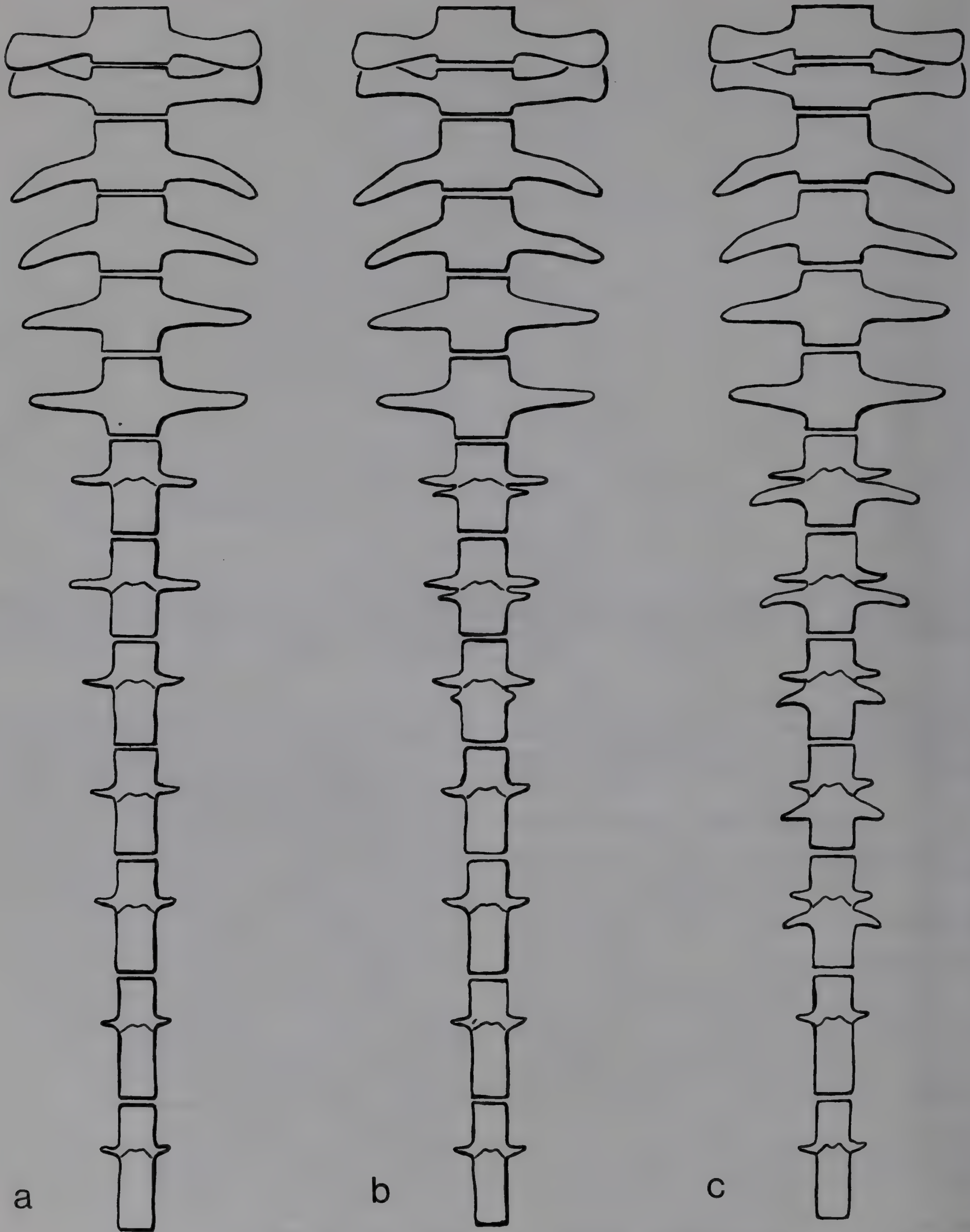


Fig. 11 Caudal vertebrae, showing principal variations in transverse processes of anterior autotomic vertebrae. a. Pattern A—a single anterior pair of processes; b. Pattern B—an anterior pair of processes followed by a parallel shorter pair; c. Pattern C—an anterior pair of processes followed by a longer posterior pair that diverge backwards. The BC pattern is intermediate between B and C: the posterior processes diverge posteriorly but are not always longer than the anterior ones. From Arnold (1973).

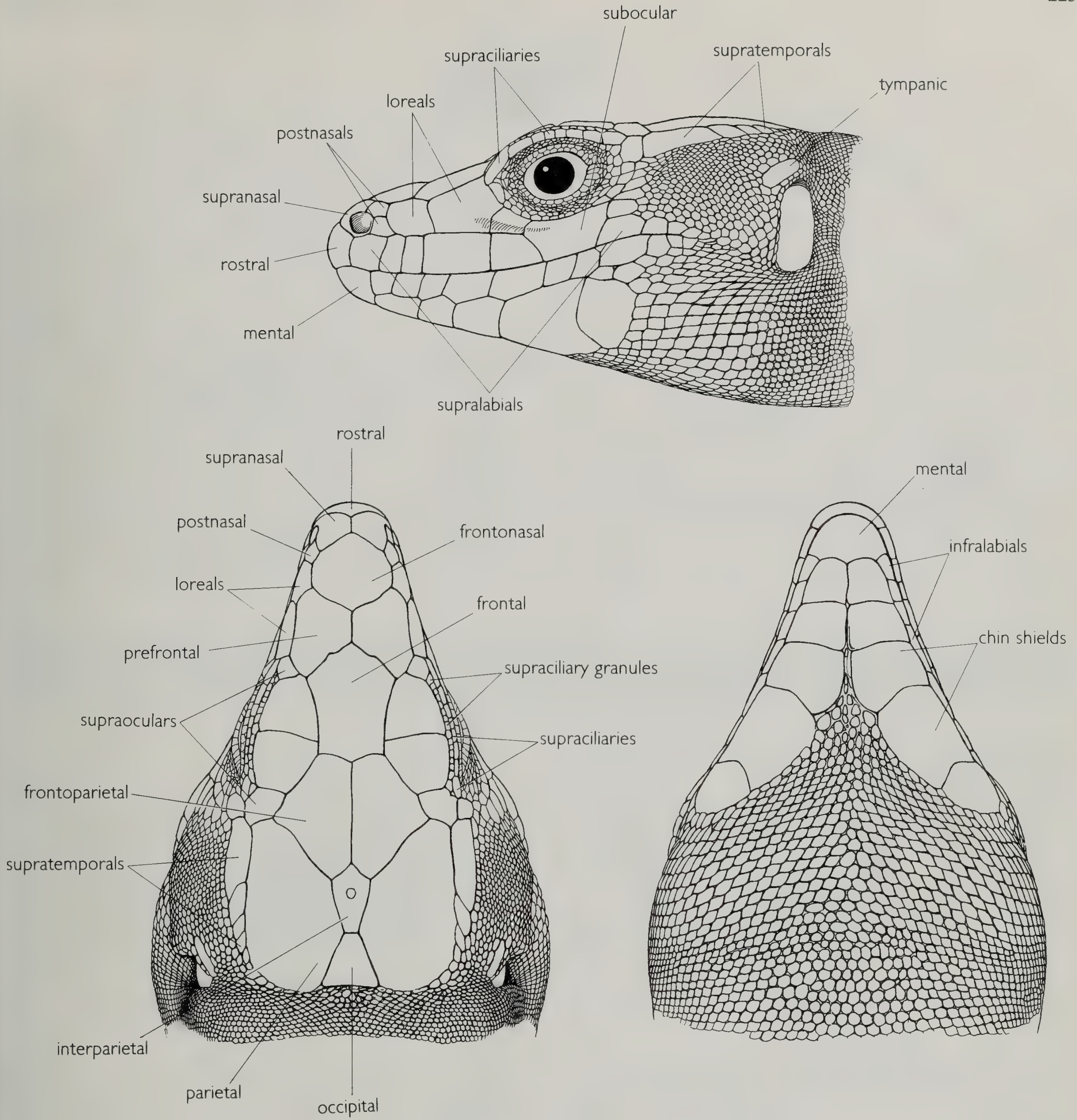

subocular
supraciliaries
supratemporals
tympanic
loreals
postnasals
supranasal
rostral
mental
supralabials
rostral
supranasal
postnasal
frontonasal
loreals
frontal
prefrontal
supraciliary granules
supraoculars
supraciliaries
frontoparietal
supratemporals
interparietal
parietal
occipital
mental
infralabials
chin shields

Fig. 12 Head scaling of *Lacerta jayakari*. From Arnold (1986*d*).

42 *Transparent 'window' in lower eye-lid* (Fig. 15). Absent (0); present (1).

43 *Masseteric scale* (an isolated large scale in temporal region). Present in at least some individuals (0); always absent (1).

44 *Chin shields*. Five or more pairs contacting the infralabials on each side (0); four pairs contacting the infralabials (1).

External features of body, limbs and tail

45.1, 45.2, 45.3 *Collar beneath throat* (a posteriorly directed transverse fold covered externally by large scales). Well developed with granules beneath (0,0,0); well developed, but no granules beneath and fixed at centre (1,0,0); weak (1,1,0); absent (1,1,1).

46 *Mid-dorsal body scales*. Small (0); large (1)

47 *Lateral body scales*. Small (0); large (1).

48.1, 48.2 *Number of longitudinal rows of ventral body scales*. Usually six (0,0); usually eight (1,0); usually ten or more (0,1).

In lacertids with large dorsal scales, it is often difficult to decide where these end and the equally large ventrals begin. But in forms with small dorsal scaling easily distinguished from the ventrals, the lateral margin of the latter corresponds closely to that of the rectus abdominis lateralis muscle. In species with large dorsal scales, this muscle will consequently

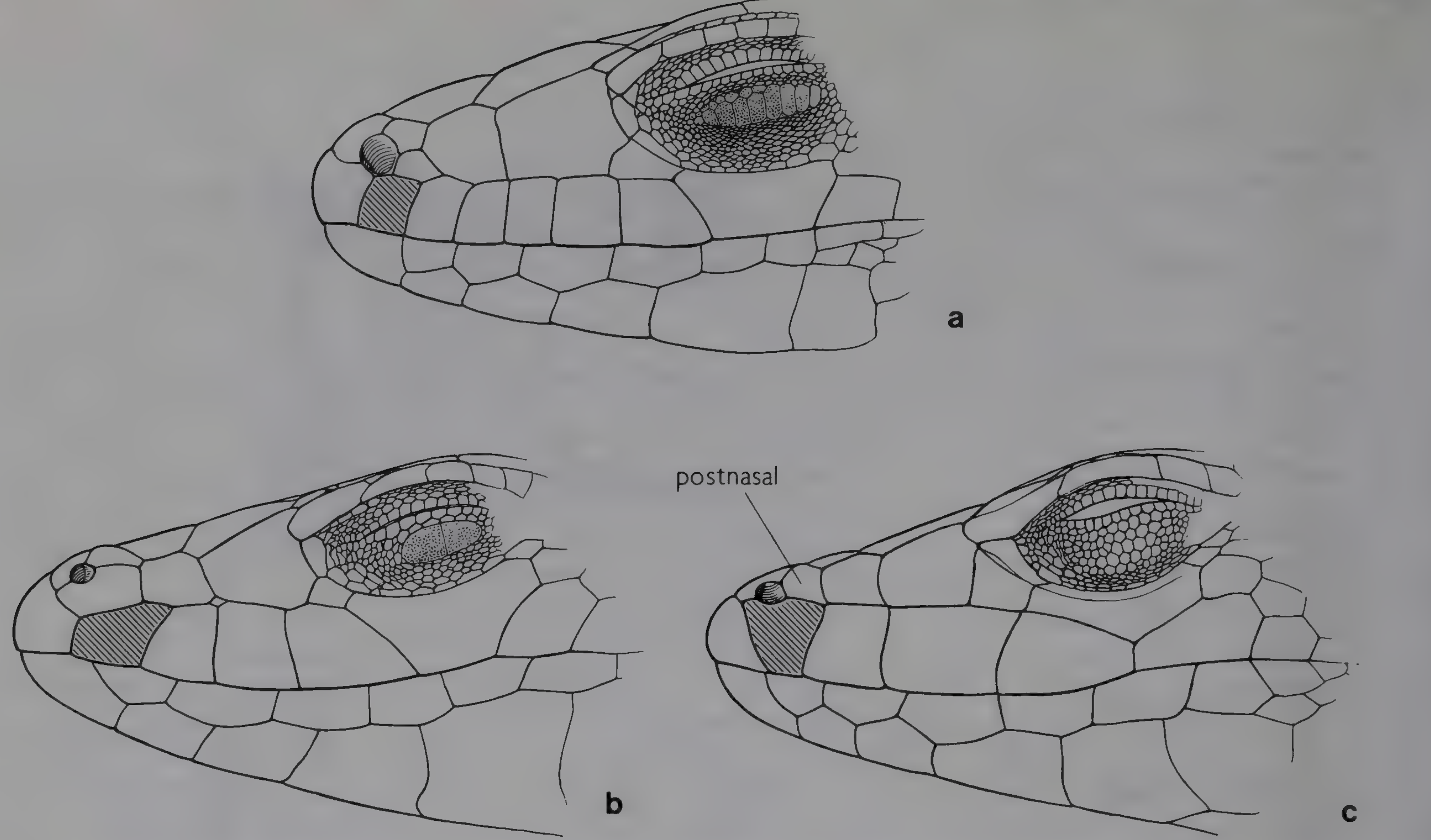


Fig. 13 Snouts of lacertid lizards, showing some variations in nasal scaling. a. First upper labial scale contacts nostril; two postnasals (*Lacerta jayakari*). b. First upper labial scale separated from nostril; two postnasals, the lower extending anteriorly to contact rostral scale (*Mesalina adramitana*). c. First upper labial scale, which has its sides converging downwards, in contact with nostril; a single postnasal (*Acanthodactylus boskianus*). First upper labial scale shaded in all cases.

be used to define the ventrals in which any scale at least partly overlying it will be included.

49.1, 49.2 *Keeling on ventral body scales*. None (0,0); outer row on each side keeled (1,0); all rows keeled (1,1).

50 *Arrangement of ventral body scales*. In more or less straight longitudinal rows (0); tessellated, so that rows tend to run diagonally (1).

51.1, 51.2 *Row of femoral pores*. Running at least two-thirds of the distance from mid-line to knee (0,0); reduced, but more than half this distance (1,0); reduced to 1–5 pores in inguinal area (0,1).

52 *Shape of scales bearing femoral pores* (Arnold, 1989, Fig. 4). Flattish (0); tuberculate (1).

53.1, 53.2 *Lateral scale rows on fingers* (Fig. 16). None (0,0); a posterior lateral row present (1,0); a posterior and an anterior row present (1,1).

54.1, 54.2 *Lateral scale rows on toes* (Fig. 16). None (0,0); a posterior lateral row present (1,0); a posterior and an anterior row present (1,1).

55 *Subdigital lamellae*. Smooth or tuberculate (0); keeled (1).

56 *Axillary mite pocket* (Arnold, 1986c). Absent (0); present (1).

57 *Post-femoral mite pocket* (Arnold, 1986c). Absent (0); present (1).

58 *Scales bordering ventral mid-line of tail*. Narrow, not much wider than adjoining scales (0); broad, much wider than adjoining scales (1).

59 *Micro-ornamentation on dorsal body scales*. Not coarsely striate (0); coarsely striate (1).

60 *Blue pigment on outer ventral scales*. Present (0); absent (1).

Various soft-part characters

61 *Tongue colour*. Predominantly dark (0); predominantly light (1).

62.1, 62.2 *Post-nasal area* (Fig. 17). Thin in horizontal section (0,0); somewhat thickened (1,0); very thick (1,1).

63.1, 63.2, 63.3, 63.4 *Nasal vestibule* (Fig. 17). Short (0,0,0,0); some elongation (1,0,0,0); vestibule overhangs posteriorly (1,1,0,0); septomaxilla largely covered by vestibular overhang (1,1,1,0); vestibular overhang covers anterior part of concha where it attaches to lateral wall of nasal cavity (1,1,1,1).

64 *Anterior extent of kidney*. Less than half length of kidney in front of sacrum (0); more than half in front of sacrum, anterior section usually expanded (1).

65 *Posterior extent of kidney*. Extends well posterior to level of vent (0); barely reaches level of vent or not at all (1).

66 *Insertion of m. retractor lateralis anterior in front of vent* (Arnold, 1984). Near mid-line (0); more laterally (1).

67 *Size of m. retractor lateralis anterior in front of vent* (Arnold, 1984): Narrow, with no fibres extending to region of vent lip (0); broad with some fibres extending posteriorly to region of vent lip (1).

68 *Some fibres of m.retractor lateralis anterior reaching base of hemipenis* (Arnold, 1984). No (0); yes (1).

69.1, 69.2 *Thoracic fascia*. None (0,0); lateral (1,0); extending to mid-line (1,1).

This structure is a superficial fascia lying just beneath the skin that overlies the thoracic region. When the fascia is present, the anterior of the m. rectus abdominis lateralis attaches to it. The fascia terminates anteriorly in the region of the lateral

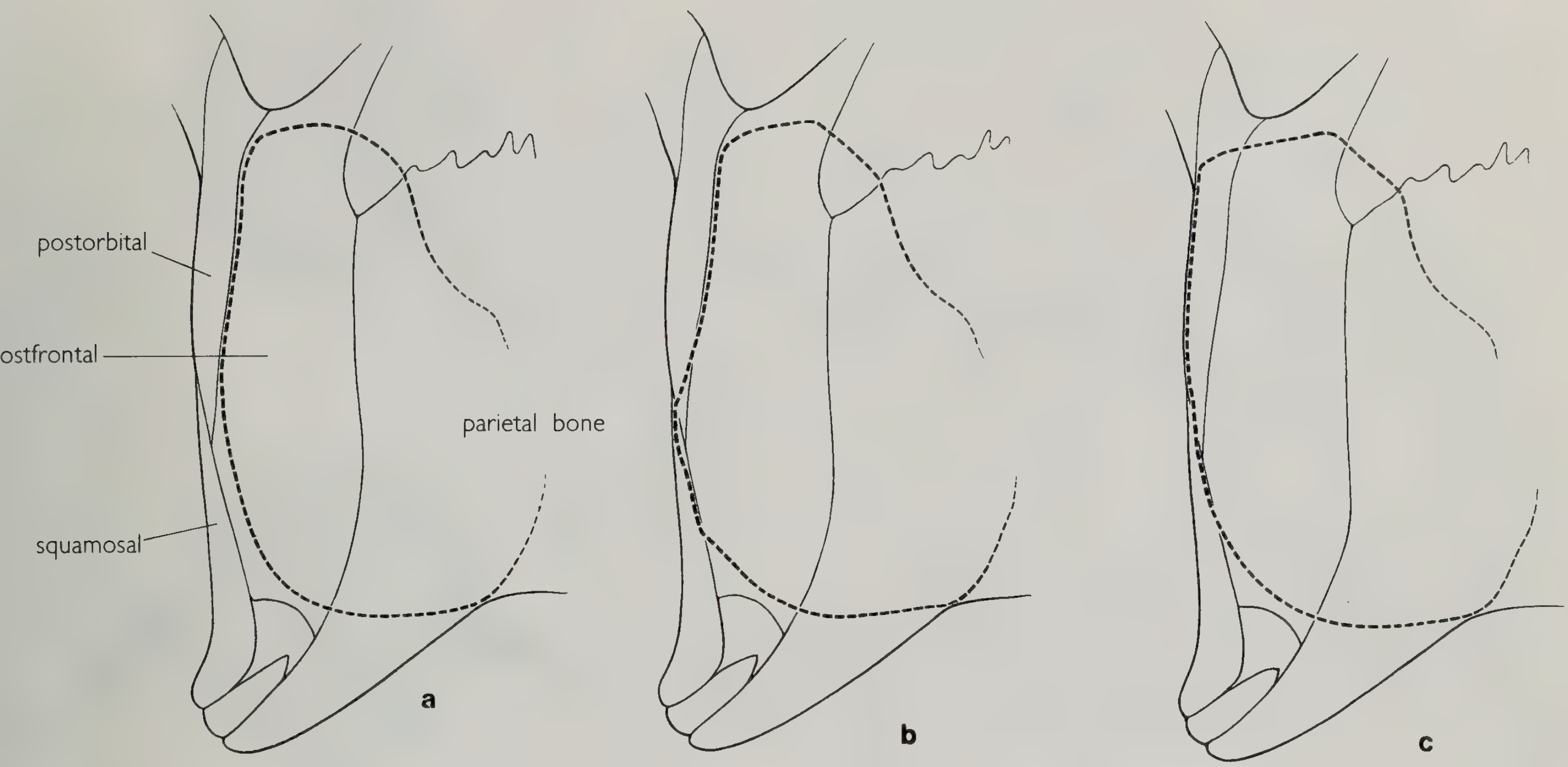


Fig. 14 Relationship between the outer margin of the left parietal scale (indicated by broken line) and the underlying bones of the skull. a. Parietal scale margin not approaching edge of parietal table; b. Parietal scale margin approaching edge of table posteriorly (on squamosal bone); c. Parietal scale margin approaching edge of parietal table posteriorly and anteriorly (on squamosal and postorbital bones).

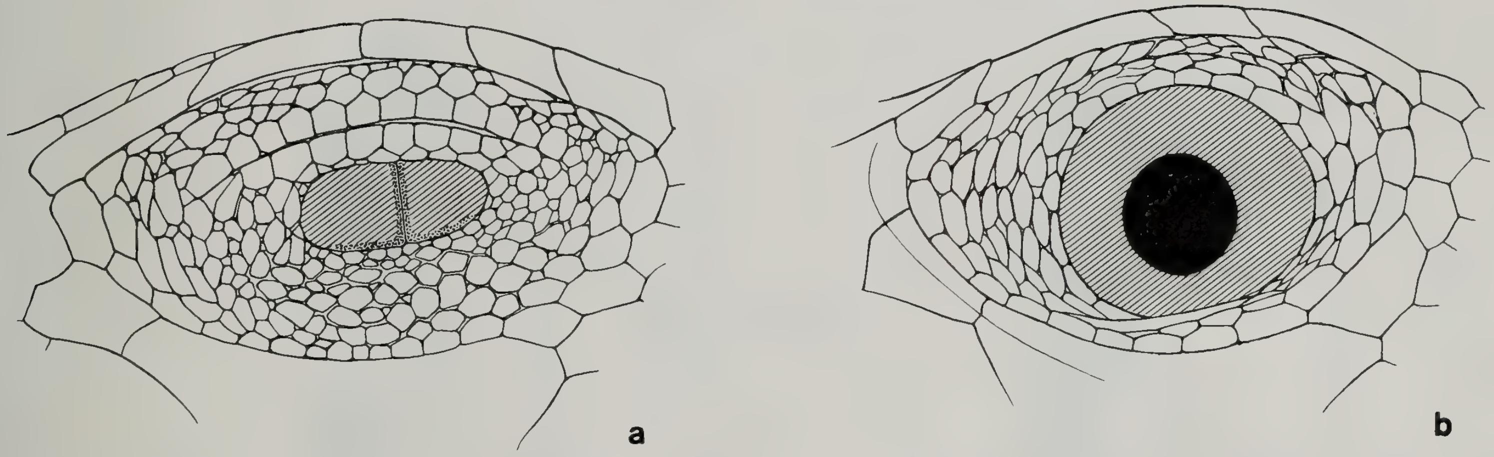


Fig. 15 Closed eyelids of left eyes, showing development of transparent 'windows'. a. Moderate, composed of two scales (*Mesalina guttulata*); b. huge, composed of a single scale, the eyelids fused (*Ophisops elbaensis*)

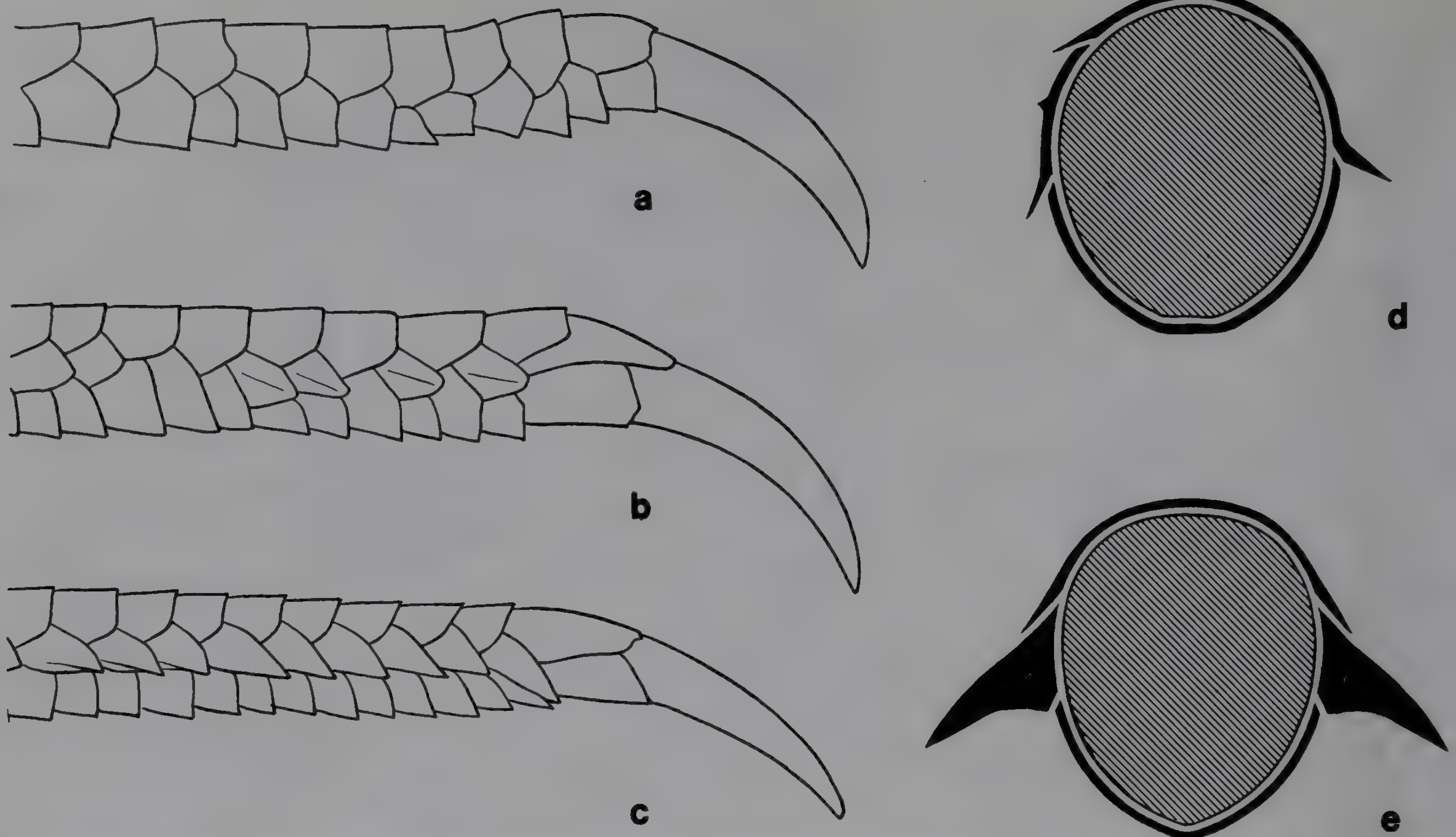


Fig. 16 Scaling on digits. a. No lateral scale row present. b, c. Partial and complete lateral row present. d. Transverse section of digit with a posterior lateral row. e. Transverse section of digit with posterior and anterior lateral rows. From Arnold (1986*d*).

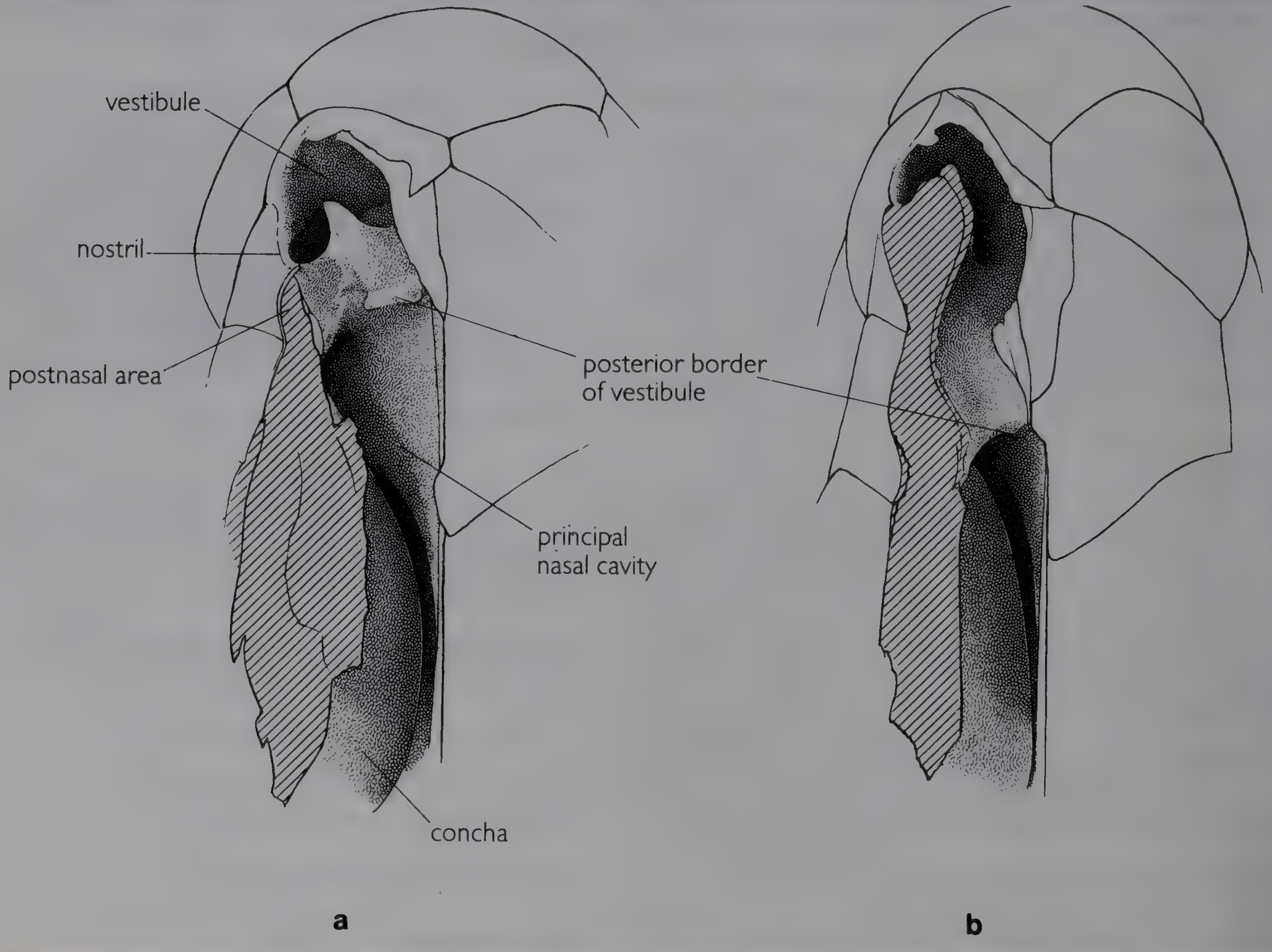

vestibule
nostril
postnasal area
posterior border of vestibule
principal nasal cavity
concha
a
b

Fig. 17 Snouts of lacertid lizards with left nasal cavity opened to show variation in thickness of postnasal region and length of nasal vestibule. a. *'Lacerta' jacksoni*; b. *Acanthodactylus cantoris*. Cut areas are hatched.

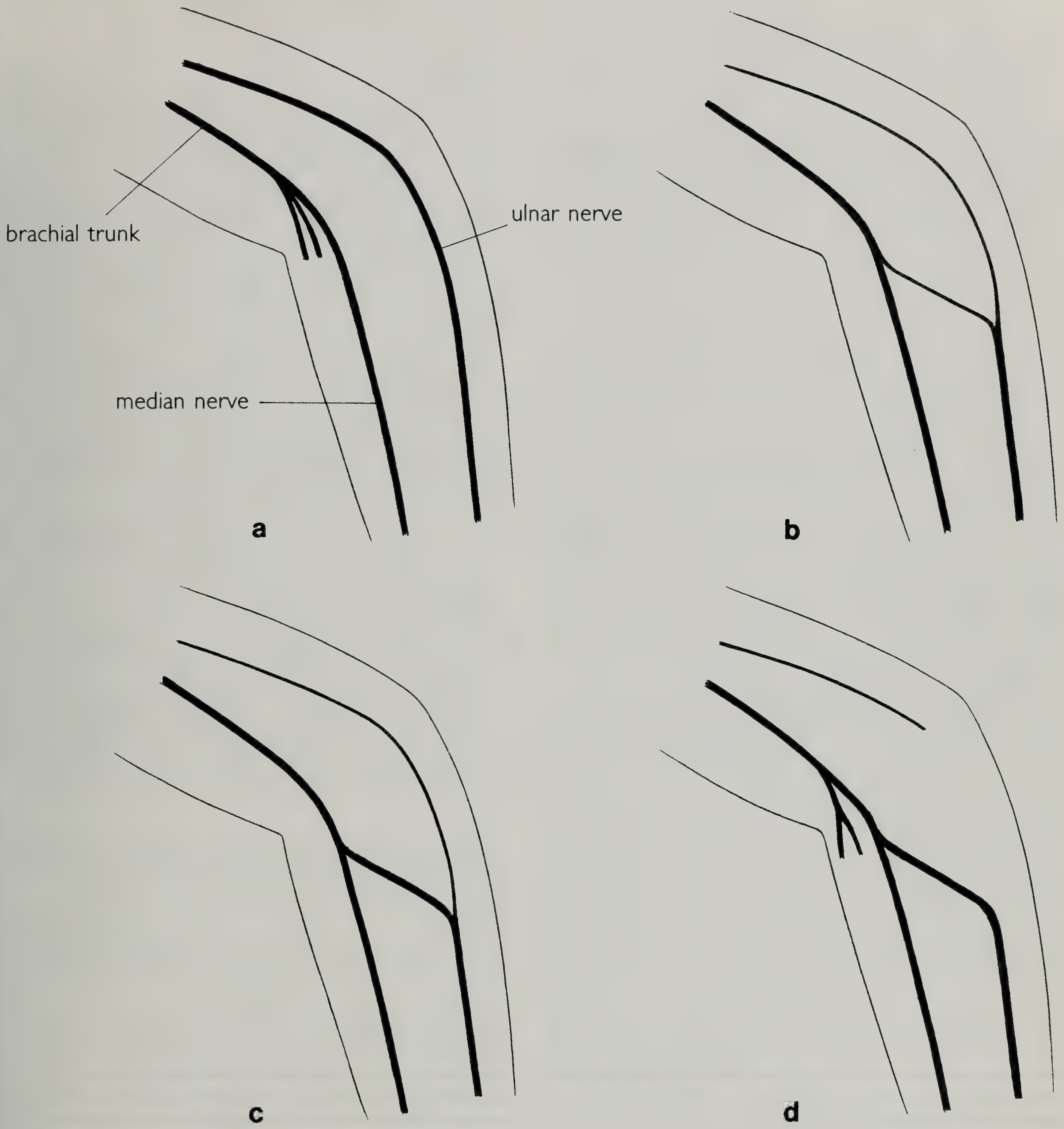


Fig. 18 Ulnar nerve patterns in lacertid lizards. a. 'Lacertide' pattern found in primitive Eurasian species. b. Intermediate pattern of *'Lacerta' jacksoni* and *Adolfus alleni*. c. Intermediate pattern of *'Lacerta' echinata* and some *Adolfus africanus*. d. 'Varanide' pattern of advanced lacertids.

arms of the interclavicle. It is frequently absent (0,0) and may be partial so that it does not cover the median area of the thorax (1,0). At its greatest extent, it reaches the midline over a considerable area of the anterior thorax (1,1).

70 *Hemipenial armature*. Absent (0); present (1).

There is evidence that absence of an armature, or its presence in only restricted form, may be a secondary condition, even though overall out-group comparison suggests that absence is the primitive state (Arnold, 1986a). This appears to be true in some species of *Pedioplanis*, *Meroles*, *Mesalina*, *Acanthodactylus* and *Eremias* in which the armature is not present in its full form. But absence of an armature may indeed be truly primitive in Palaearctic forms assigned to *Lacerta*, *Algyroides*, *Psammodromus Gallotia*, *Podarcis*, *Takydromus* and *Platyplacopus*. A contrary interpretation has been proposed elsewhere for the first five of these genera (Arnold, 1986a), but a simpler explanation seems more appropriate.

71 *Cross section of lobes in unreverted hemipenis*. Simple (0); flattened and complexly folded (1).

72 *Length of hemipenial lobes*. Relatively short (0); relatively long (1).

Because this character and the following one are difficult to assess in uneverted hemipenes where the lobes are complexly folded, they have been recorded only in the Palaearctic forms where lobes are nearly always simple and sac-like

73 *Lips on hemipenial lobes*. Moderate or quite small (0); large (1).

74 *Inner connectors arising close to the tips of the hemipenial clavulae*. No (0); yes (1).

75 *Medial side of hemipenis and armature reduced*. No (0); yes (1).

76 *Lateral side of hemipenis and armature reduced*. No (0); yes (1).

77 *Large pointed papillae on hemipenial lobes* (Arnold, 1973). Absent (0); present (1).

78.1, 78.2 *Hemipenial microornamentation*. Crown-shaped tubercles (0,0); bicuspid tubercles (1,0); simple spines (1,1).

Hemipenial sheath. Arnold (1984) noted that most lacertids examined had a membranous sheath around the uneverted hemipenis and associated m. retractor magnus, but that this is missing in *Takydromus*. Investigation of more material makes it apparent that this feature is very variable in its development, so that in some cases it is very difficult to know if it is really present or not. Because of this problem of scoring, it is not included in the analysis presented here.

79 *Female genital sinus*. Bilobed (0); unlobed (1).

80 *Exit of oviducts into genital sinus*. Ventrally, some way from tip(s) of sinus (0); at or near tip(s) or dorsally (1).

81.1, 81.2 *Course of ulnar nerve* (Fig. 18). 'Lacertide' (0,0); intermediate (1,0); 'varanide' (1,1).

Julien & Renous-Lécuru (1972) discuss two patterns of innervation of the lower forelimb in lizards. In the more primitive ('lacertide') condition, the ulnar nerve is completely independent of the brachial trunk and the nerves originating from it, and follows a superficial course in the lower limb (Fig. 18a). In the more advanced ('varanide') condition, there is a common trunk in the upper arm which includes all the fibres of the ulnar nerve that serve the lower limb; these separate only distal to the elbow (Fig. 18d). The authors correctly report both conditions in the Lacertidae, but intermediates also exist. In '*Lacerta*' *jacksoni* and *Adolfus alleni* some fibres of the ulnar nerve follow the 'lacertide' course while others follow the 'varanide' one, so that an independent ulnar nerve runs from the upper to the lower forelimb but receives additional fibres in the lower limb which form a slender bridge from the brachial trunk (Fig. 18b). '*Lacerta*' *echinata* and some *Adolfus africanus* are similar but more fibres follow the 'varanide' route, so that the bridge is thicker, and the upper part of the ulnar nerve more attenuated (18c).

82 *Lateral septum on bodenaponeurosis*. Present (0); absent (1).

Rieppel (1980) surveyed the jaw musculature of various scincomorph groups and believed that lack of a lateral septum on the bodenaponeurosis, and consequent lack of intersection of either the medialis or superficialis layers of the external adductor muscle, is a specialised feature of the Lacertidae. He is perfectly correct about this condition being present in the four species he examined, but a wider survey shows that it is a minority state and most lacertids do have a lateral septum.

Behaviour

83 *Voice*. Usually mute (0); squeak frequently (1). See Böhme, Hutterer & Bings (1985).

84 *Copulatory position*. Male grasps female by flank (0); male grasps female by neck or mid-back (1).

Böhme and Bischoff (1976) regard holding the neck of the female during copulation as primitive in the Lacertidae, on the basis of the wide distribution of this behaviour in other lizards. However, the usual alternative, biting the flank, also has quite a broad distribution and in scincomorphs occurs in some Scincidae (for instance *Ablepharus*—Rotter, 1962) and Teiidae (*Cnemidophorus sexlineatus*—Smith, 1946; *C. gularis*—Walker, Cordes & Paulissen, 1987). So evidence from outgroup analysis is equivocal. Within the Lacertidae, neck biting is a rare and scattered condition suggesting it may be derived rather than primitive. It occurs in *Gallotia* (Böhme & Bischoff, 1976), *Psammodromus algirus* (Birkenmeier, 1951; Bosch, 1986), *Lacerta jayakari* (Böhme & Bischoff, 1976; Bischoff, 1981), *Lacerta vivipara* but only as a preliminary to grasping the flank (Mortensen, 1887), *Aporosaura anchietae* (Louw & Holm, 1972) and *Mesalina olivieri* (Bons, 1959). In *Psammodromus hispanicus* the flank may be grasped first and then the male holds the skin of the central back and sometimes further forward (In den Bosch, 1986). At least some other species of the holophyletic genus *Mesalina* grasp the flank of the female (*M. adramitana*, personal observations; *M. guttulata*, W. Ross, personal communication) and the use of outgroup analysis within the family, once the relationships of *Mesalina* and *Aporosaura* are established (p. 000), indicate that neck biting is derived in these groups. The same appears to be true in *Gallotia* and *Psammodromus algirus* (p. 000) and probably elsewhere.

METHODS OF ANALYSIS

As well as informal approaches, the data set (Appendix 2) was investigated by computer in two different ways: parsimony analysis and compatibility analysis.

Parsimony analysis

Parsimony analysis was carried out using the 2.4 version of the PAUP (Phylogenetic Analysis Using Parsimony) programme (Swofford, 1985). This produces one or more trees with the minimum number of character state changes (steps). It is a Wagner method of parsimony analysis in that forward and reverse changes have equal probability. The tree was rooted by the inclusion of a hypothetical common ancestor with 0 scores for all characters. When large numbers of taxa were analysed, the following options of the PAUP programme were initially used: ADSEQ = CLOSEST, HOLD = 25, SWAP = GLOBAL, MULPARS, ROOT = ANCESTOR, OPTIMISATION = MINF, BLRANGE, CSPOSS. ADDSEQ and HOLD options were subsequently varied, a process which sometimes produces shorter trees, but none were found. For less than 12 taxa the 'Branch and Bound' method of Hendy & Penny (1982) was employed, instead of GLOBAL and MULPARS. For less than nine taxa the ALLTREES option was used, which is guaranteed to find minimum length trees. In some cases, where numerous alternative trees were found, consensus trees were computed using Swofford's CONTREE (Consensus Tree) programme. The option used was STRICT, which uses the 'strict' method of Rohlf (1982).

In parsimony analysis, variable scores have been treated in most cases as if they were primitive (0) scores, on the assumption that the existence of derived (1) scores in groups where both 0 and 1 occur is due to homoplasy. The only exceptions are cases where there is internal evidence within the taxonomic unit concerned that the primitive state in the group is 1. This is true of characters 3.1, 55, 64, 70 and 71 in *Meroles*, 70 and 71 in *Pedioplanis* (see Arnold, in press); and 15 in *Ophisops-Cabrita*.

In some cases, adjustment of variable scores makes characters invariant or results in only one taxon having the derived (1) condition. Such characters, where the derived state is not shared by two or more taxonomic units, contribute nothing to analysis and can be ommitted. Thus, for the total Lacertidae, this is true for 20, 28, 36, 37, 40.1, 41.1, 41.2, 50, 51.2, 53,2, 54.2, 56, 57, and 76 (n=14), reducing the data set to 98 binary characters.

Compatibility analysis

Compatability analysis was carried out using the programme of Gauld & Underwood (1986). This conducts Le Quesne tests (Le Quesne, 1969) on all characters in which both states occur more than once, and the frequency of failure of each character (that is incompatibility with other characters) is compared with that expected on a random basis. The characters are then ranked in ascending order of their randomness ratios, i.e. the ratio of observed incompatibilities to those expected on the null hypothesis of random distribution of the states of the characters. As already noted, it is not necessary to know the polarity of the characters concerned to do this.

Because the score of a reliable character may be adversely influenced by association with unreliable ones during the Le Quesne testing, a second procedure, known as 'boil down' is carried out. This removes the character with the highest randomness ratio and reruns the Le Quesne test and ranking procedure, often resulting in a different ranking order. Then, the character with the highest randomness ratio in this reduced set is removed and the process repeated, and so on until only a compatible set of the highest scoring characters is left. This set is expected to give good indications of relationship of the taxa concerned, provided it contains enough characters. Further information on relationships may be given by the inclusion of any additional characters that were not amenable to Le Quesne testing because the primitive state occurs in one taxon only. Other characters, considered in the reverse order of their removal during the 'boil down' procedure, may also contribute to analysis. In some cases, they can be substituted for members of the compatible set, or some small degree of homoplasy may be tolerated.

Some characters are likely to score badly during the initial 'boil down' because they are homoplastic. However, if a well substantiated subgroup of the one under investigation can be discerned, it is possible that a character present in the subgroup and outside it may give good information in one or both these areas in spite of its overall homoplasy. In such cases the relevant subgroups can be reanalysed separately.

Resolution of conflicts

Where parsimony and compatibility methods disagree, or when trees produced by parsimony differ from each other in detail, so there are alternative relationships for particular taxa, the evidence for the alternatives is compared. In attempting to resolve such conflicts, not only is the number of derived features on each side taken into account, but also their general lability, judged by the number of state changes the character makes in the total provisional lacertid phylogeny. Combining these factors involves a degree of subjectivity, but is more realistic than simply confining decisions to the number of binary characters supporting each version of relationships.

Comparison of methods of analysis

Parsimony and compatibility methods used here are in principle quite different. The Wagner parsimony approach aims to minimise the total number of steps in a tree and consequently minimises the number of homoplasies (parallelisms and reversals). The method is open to a number of criticisms as a means of estimating the phylogeny of a group. 1. To begin with, virtually all analyses of large systematic data sets involve considerable homoplasy, even when the method aims to minimise this. Given that homoplasy seems common in the evolution of animal groups, it is difficult to justify the lowest level as being most likely. 2. As all characters are given equal weight, it is possible that states correlating with the real course of evolution may sometimes be outweighed by labile homoplasious features, especially if these tend to be correlated. 3. The method sometimes produces a multiplicity of trees of equal length and there is no simple way of differentiating these. 4. Polarities have to be decided at the commencement of analysis. 5. With large numbers of taxa, the method cannot guarantee to find the shortest tree.

The compatibility method used here compares as follows. 1. There are no assumptions of how evolution proceeds, for instance, the method does not necessarily minimise homoplasy. 2. The method aims to differentiate compatible characters that are likely to show the structure of a phylogeny and to arrange the remainder in an order of increasing likely homoplasy, which means that the most noisy characters can be omitted from phylogeny reconstruction if required, so that swamping of real structure is less likely. 3. The method does not produce a multiplicity of trees. However, it often fails to provide a total structure for the phylogeny. 4. Only a few polarities need to be decided by external means (p. 215). 5. Like parsimony analysis, there is no guarantee that the shortest tree will be found. The compatibility method might be expected to fail in cases where most characters were somewhat homoplastic, so that only a small fully compatible set could be discerned, or none at all. Secondary analysis can sometimes alleviate this problem.

In the present case, parsimony and compatibility methods do not produce results that are radically different. As will be seen, in the Ethiopian and Saharo-Eurasian clade, where data show considerable order, both identify the same essential structure, although parsimony tends to show more detail. On the other hand, when dealing with primitive Palaearctic lacertids, in which there is considerable character conflict, both fail to make much impact, identifying the same relationships but failing to discern a robust general structure. So, in spite of their different rationales, the methods may not necessarily differ much in result. This was also found in a detailed analysis of Equatorial African lacertids (Arnold, 1989).

PRELIMINARY DIVISION OF THE LACERTIDAE

Parsimony analysis of 98 characters for the whole Lacertidae produced over 100 trees of 333 steps and a consistency index of 0.294. The large number of trees indicates considerable homoplasy. Examination of a selection of these shows that *Lacerta jayakari* etc, all the Ethiopian taxa plus four advanced genera from Saharan and Eurasian areas, viz. *Acanthodactylus*, *Eremias*, *Mesalina* and *Ophisops-Cabrita*, from a clade which is derived from a paraphyletic assemblage of primitive Palaearctic and Oriental forms. This clade is relatively stable, but the arrangement of the remaining taxa is very variable. A consensus tree confirms this: the African and advanced section shows considerable structure, while little is discernible in the primitive Palaearctic and Oriental forms.

Fig. 19a

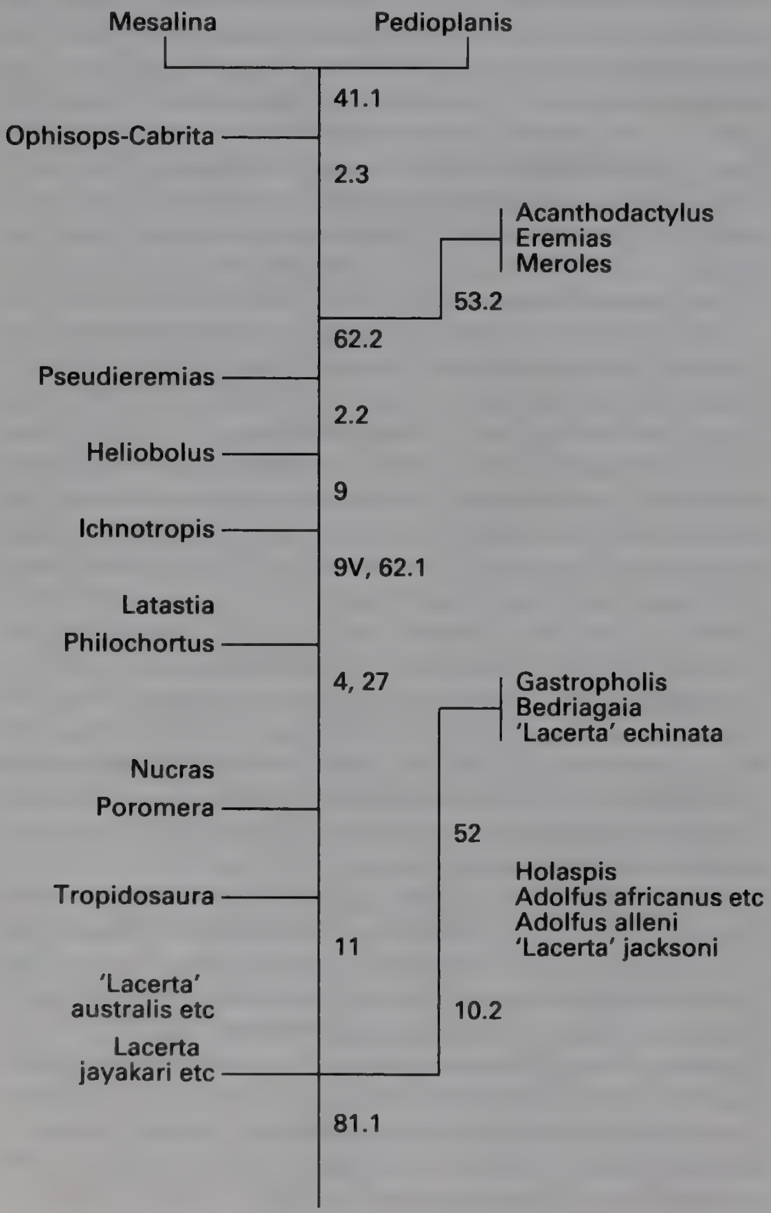
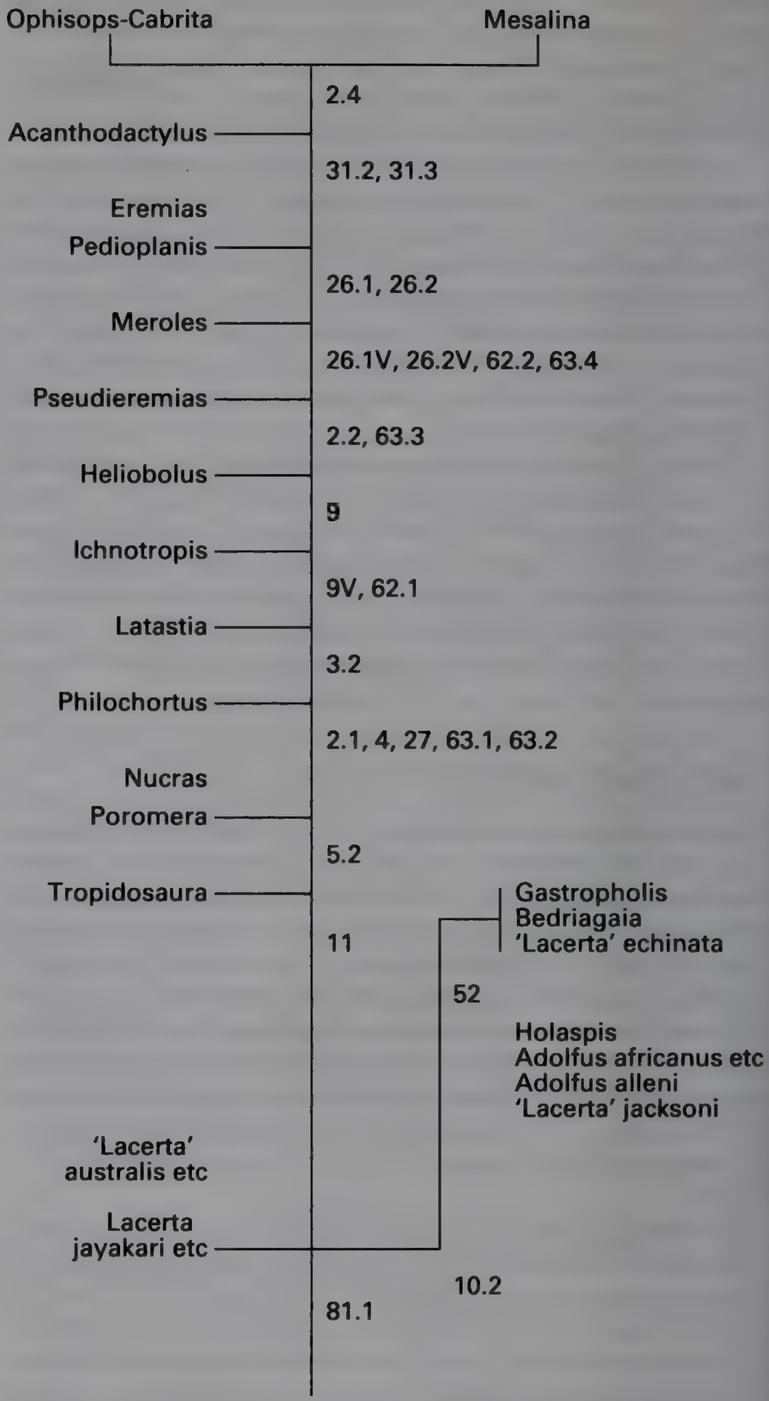

Mesalina
Pedioplanis
41.1
Ophisops-Cabrita
2.3
Acanthodactylus
Eremias
Meroles
53.2
62.2
Pseudieremias
2.2
Heliobolus
9
Ichnotropis
9V, 62.1
Latastia
Philochortus
4, 27
Gastropholis
Bedriagaia
'Lacerta' echinata
Nucras
Poromera
52
Holaspis
Adolfus africanus etc
Adolfus alleni
'Lacerta' jacksoni
Tropidosaura
11
'Lacerta' australis etc
10.2
Lacerta jayakari etc
81.1

Fig. 19b


Ophisops-Cabrita
Mesalina
2.4
Acanthodactylus
31.2, 31.3
Eremias
Pedioplanis
26.1, 26.2
Meroles
26.1V, 26.2V, 62.2, 63.4
Pseudieremias
2.2, 63.3
Heliobolus
9
Ichnotropis
9V, 62.1
Latastia
3.2
Philochortus
2.1, 4, 27, 63.1, 63.2
Nucras
Poromera
5.2
Tropidosaura
Gastropholis
Bedriagaia
'Lacerta' echinata
11
52
Holaspis
Adolfus africanus etc
Adolfus alleni
'Lacerta' jacksoni
'Lacerta' australis etc
Lacerta jayakari etc
10.2
81.1

Compatability analysis of the whole data set gives an overall randomness ratio of 0.87, again indicating that considerable homoplasy exists. The 'boil down' process produces a compatible set of 17 characters, with one alternative (53.1). This and three others (40.1, 43, 53.2) involve considerable numbers of variable (V) scores and are therefore discarded. The remaining characters generate the arrangement shown in Fig. 19a, which again associates *Lacerta jayakari* etc and all the Ethiopian and advanced Saharo-Eurasian taxa. In the remainder of the Lacertidae, the primitive Palaearctic and Oriental forms, compatibility produces no certain assocations. This, like the variable results produced by parsimony analysis, indicates a lack of robust overall structure in the data set for these taxa.

The Lacertidae can therefore be divided into two sections for convenience: a holophyletic, mainly African group with advanced forms extending into Eurasia and a primitive Palaearctic and Oriental assemblage that is very probably paraphyletic. These will be analysed further separately.

Fig. 19c

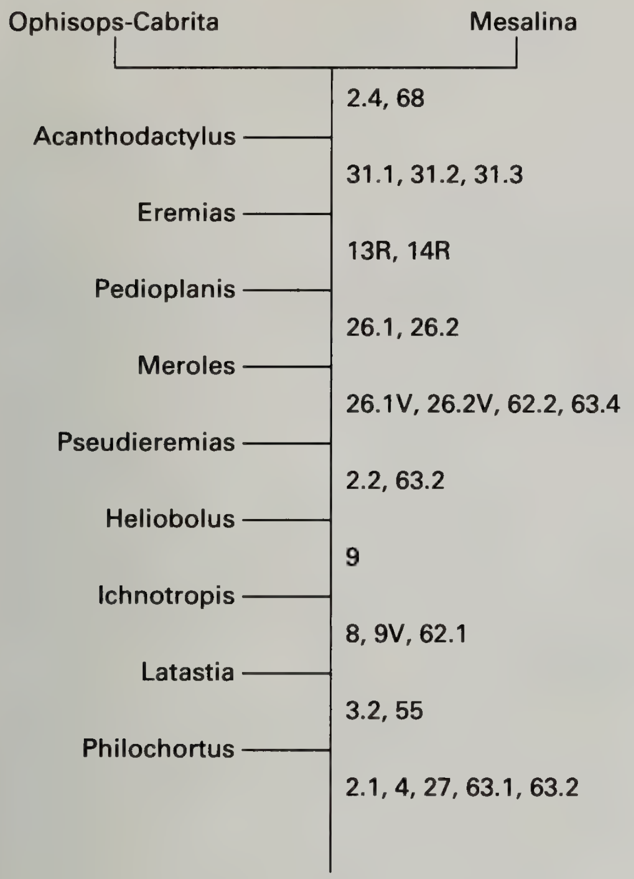


Fig. 19 Compatibility analyses of the Lacertidae. a. Total lacertids; b. Ethiopian and advanced Saharo-Eurasian forms; c. *Philochortus* and its derived relatives. V – variable characters

PRIMITIVE PALAEARCTIC AND ORIENTAL LACERTIDS

Parsimony analysis

Parsimony analysis was applied to the primitive Palaearctic and Oriental lacertids with a hypothetical ancestor of the Ethiopian and advanced Saharo-Eurasian clade included in the data set. Characters that have no shared derived states within this assemblage were eliminated, namely 2.2, 2.3, 2.4, 3.2, 4, 5, 6.1, 6.2, 7, 8, 9, 10.1, 10.2, 11, 13, 14, 15, 16, 17, 20, 21, 23, 25, 26.2, 26.3, 27, 28, 34, 36, 37, 40.1, 40.2, 41.1, 41.2, 45.3, 49.1, 49.2, 50, 51.1, 51.2, 52, 53.1, 53.2, 54.1, 54.2, 55, 56, 57, 62.1, 62.2, 65, 69.2, 74, 75, 76, 81.2. This left a set of 56 binary characters. Over 100 trees of 134 steps and a consistency index of 0.410 were produced.

As the evidence for polarities of some characters involves a marked degree of conflict, particularly between outgroup and other indicators (p. 215), the process was repeated with the following polarities changed. Run 2: characters 22.2, 28, 32 and 43. Run 3: characters 22.2, 28, 31.2, 31.3, 32, 43 and 84. Run 4: characters 22.1, 22.2, 28, 31.1, 32 and 43. All these modifications produced trees with more steps than those in which the original polarities were used, so the latter may well be correct. Characters 22.2, 32 and 43 turn out to be substantially homoplasious, which suggests they are quite labile in lacertids and that the outgroup indicators of polarity could be wrong (p. 214).

As expected from the preliminary analysis of the whole Lacertidae, a consensus tree derived from the latter has relatively little structure with a basal polychotomy of 14 branches. The only associations are *Gallotia*, *Psammodromus*, *Lacerta parva* etc. and *L. brandtii*; *Lacerta princeps* with *L. lepida* etc. and these with the *Lacerta agilis* group; *Lacerta dugesii* with *L. perspicillata*; *Lacerta graeca* with *L. oxycephala*; and *Lacerta jayakari* etc. with the hypothetical ancestor of the Ethiopian and advanced Saharo-Eurasian clade.

Examination of a selection of the numerous trees produced by parsimony analysis, both with original and modified polarities, shows that, while not necessarily universal and therefore not represented in consensus trees, certain additional associations are very frequent; for instance, *Podarcis*, *L. andreanskyi*, the *L. dugesii-L. perspicillata* clade, *L. danfordi* and *L. laevis*.

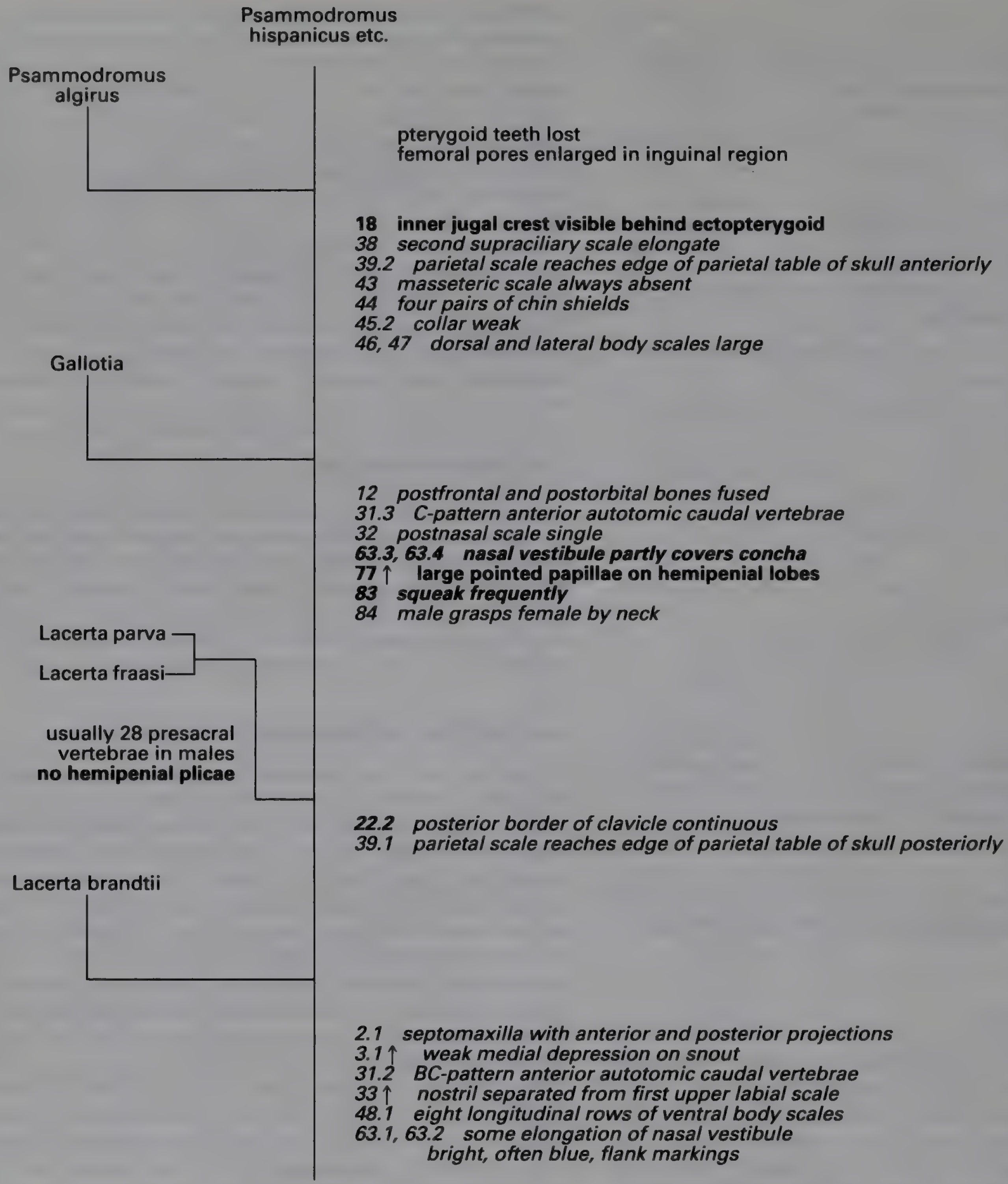
Compatibility analysis

Again, this method fails to produce a robust detailed picture of relationships but, like parsimony, supports the *Gallotia-Psammodromus* association strongly and allies these with *L. parva* etc. and *L. brandtii*. It also allies *L. dugesii with L. perspicillata*, *L. graeca with L. oxycephala* and *L. jayakari* with the Ethiopian and advanced Saharo-Eurasian clade. In addition, *L. vivipara* is associated with the latter groups.

Karyological and biochemical evidence

The lack of consistent structure in the data set for primitive Palaearctic lacertids probably results from the amount of morphological change which has occurred being relatively restricted and often repetitive, so that there are high levels of homoplasy. Given the poor quality of the evidence from general morphology, other sources of information must also be considered. Although gross karyology is often uninformative in lacertids (see for example Kupryanova, 1986), it is not always so and interesting information on the fine structure of lacertid chromosomes has also recently been reported, particularly C-banding, chromosome number and the location of the nucleolar organiser (Odierna, Olmo & Cabror, 1985; Olmo, Odierna & Cabror, 1986; Odierna, Olmo & Cobror, 1987; Cano, Baez, Lopez-Jurado & Ortega, 1984; Lopez-Jurado, Cano & Baez, 1986). Some well supported species groups seem to be consistent for the latter feature, but it is not possible to be sure when the condition can be regarded as a synapomorphy, as the primitive state is not certainly established. This is also true for chromosome numbers, where it has been suggested that the high counts of 40 and 42 found in some *Takydromus sexlineatus* and 40 in *Gallotia* are primitive relative to the 38 chromosomes present in most lacertids that have been checked, although distribution of other features suggests the reverse. A wider survey of these characters in the Lacertidae may resolve matters.

Attempts have also recently been made to determine relationships of lacertids, especially primitive Palaearctic ones, by chemical means including protein electrophoresis and immunology, particularly of albumins (Engelmann & Schäffner, 1981; Engelmann, 1982; Guillaume and Lanza, 1982; Lanza and Cei. 1977; Lanza, Cei and Crespo, 1977; Lutz and Mayer, 1984, 1985; Lutz, Bischoff and Mayer, 1986; Mayer, 1981, 1986. Mayer and Tiedemann, 1980*a*, 1980*b*, 1981, 1982; Borisov & Orlova, 1986; Busack & Maxson, 1987). In some cases, this chemical evidence supports



pterygoid teeth lost
femoral pores enlarged in inguinal region

18 inner jugal crest visible behind ectopterygoid
38 second supraciliary scale elongate
39.2 parietal scale reaches edge of parietal table of skull anteriorly
43 masseteric scale always absent
44 four pairs of chin shields
45.2 collar weak
46, 47 dorsal and lateral body scales large

12 postfrontal and postorbital bones fused
31.3 C-pattern anterior autotomic caudal vertebrae
32 postnasal scale single
63.3, 63.4 nasal vestibule partly covers concha
77 ↑ large pointed papillae on hemipenial lobes
83 squeak frequently
84 male grasps female by neck

22.2 *posterior border of clavicle continuous*
39.1 parietal scale reaches edge of parietal table of skull posteriorly

2.1 septomaxilla with anterior and posterior projections
3.1 ↑ weak medial depression on snout
31.2 BC-pattern anterior autotomic caudal vertebrae
33 ↑ nostril separated from first upper labial scale
48.1 eight longitudinal rows of ventral body scales
63.1, 63.2 some elongation of nasal vestibule
bright, often blue, flank markings

Fig. 20 Relationships of *Psammodromus*, *Gallotia*, *Lacerta parva etc and Lacerta brandtii.* Character transformations supporting relationships are differentiated as follows.

bold—transformation unique in lacertids
bold italic—transformation unique in primitive Palaearctic and Oriental lacertids
roman—transformation occurring more than once in primitive Palaearctic lacertids, but not in Ethiopian and advanced Saharo-Eurasian forms.
roman italic—transformation occurring more than once in primitive Palaearctic lacertids and also in Ethiopian and advanced Saharo-Eurasian forms.
↑ – character that subsequently reverses
R – character reversal

groupings established on the basis of morphology but it sometimes conflicts with them. Also, alternative interpretations of the results have been suggested (Busack & Maxson, 1987). The following discussion, while based largely on morphology, take these new karyological and chemical data into account.

Gallotia, Psammodromus and their likely relatives

Both compatibility analysis and parsimony techniques associate these forms in the way shown in Fig. 20, in which a few characters additional to the basic lacertid data set have been incorporated. The relationship of *Gallotia* and the species of *Psammodromus* is quite strongly supported and there is also limited corroborative evidence from protein electrophoresis (Lutz, Bischoff and Mayer, 1986). *P. algirus* lacks the distinctive large pointed papillae on the hemipenial lobes (77) of other *Psammodromus* and *Gallotia*, but this may well be a secondary loss, perhaps associated with the narrowing of the hemipenial lobes found in this species (Arnold, 1973, 1986*a*).

A direct relationship between the *Psammodromus hispanicus* group and the markedly different *P. algirus* is also supported by several features, in particular the unique modified jugal (18), and also the elongate second supraciliary scale (38) and the presence of only four pairs of chin shields (44); while not unique, these latter characters have a very restricted distribution among primitive Palaearctic lacertids. The available immunological evidence for this association is weak and protein electrophoresis does not suggest that the two sections of *Psammodromus* are closer to each other than each is to *Gallotia* (Lutz, Bischoff and Mayer, 1986).

In fact there are a number of characters that support a direct relationship between *P. algirus* and *Gallotia*, including lack or poor development of a septum on the bodenaponeurosis (82), long hemipenial lobes (72), hemipenial micro-ornamentation of simple spines (78.2), ten or more longitudinal rows of ventral scales (48.2), and perhaps a reversion to a primitive feature, contact between the nostril and the first upper labial scale (33). However, fewer characters support this association than that between the two parts of *Psammodromus* and all of them occur elsewhere among primitive Palaearctic lacertids. Ten longitudinal rows of ventrals could easily be derived from the eight found in other *Psammodromus*. While not being interpreted as supporting a direct relationship between *P. algirus* and *Gallotia*, these presumed parallelisms emphasize the general affinity of the latter and the whole of *Psammodromus*.

It has been suggested that many of the features of *Gallotia*, and consequently of *Psammodromus*, are plesiomorphic (Böhme, Hutterer & Bings, 1985). As such they could not be used to support relationships. However, when polarities were altered for these characters (Run 3, p. 231) and parsimony analysis carried out, *Gallotia* and *Psammodromus* were still firmly associated and neither was placed near the base of trees produced.

The holophyly of *Gallotia* is quite well supported, but relationships within the genus involve a conflict between morphology and chemical evidence. *G. galloti*, *G. simonyi* and *G. stehlini* have most apparent physical synapomorphies (Fig. 21), while *G. atlantica* shares only ossification of the temporal scales (19) with the two latter species, and only lateral extension of the parietal scale (39.2) with *G. galloti*. In contrast, albumin immunology and protein electrophoresis suggest that the closest relationship is between *G. atlantica* and *G. galloti* (Lutz, Bischoff & Mayer, 1986). A preliminary numerical phylogenetic analysis was conducted by Thorpe, Watt and Baez (1985), who constructed a Wagner tree based on the range coded means of 23 scalation and 24 adjusted body proportions for *G. atlantica*, *G. galloti* and *G. stehlini*. A mid-point rooted cladogram indicates that *G. galloti and G. stehlini* are most closely related, but the authors regard the result as equivocal.

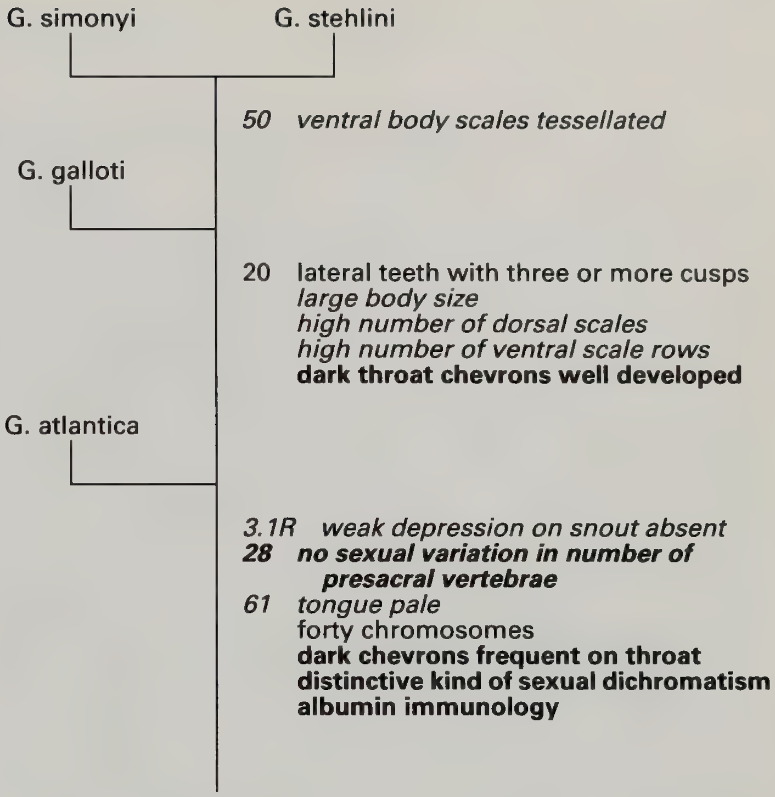

G. simonyi
G. stehlini
50 ventral body scales tessellated
G. galloti
20 lateral teeth with three or more cusps
large body size
high number of dorsal scales
high number of ventral scale rows
dark throat chevrons well developed
G. atlantica
3.1R weak depression on snout absent
28 no sexual variation in number of presacral vertebrae
61 tongue pale
forty chromosomes
dark chevrons frequent on throat
distinctive kind of sexual dichromatism
albumin immunology

Fig. 21 Relationships of the species of *Gallotia*. For further explanation, see caption of Fig. 20

Engelmann and Schäffner (1981), on the basis of immuno-electrophoresis, suggest that *L. parva* is related to *L. princeps* and *L. lepida*, but morphology supports relationship with *Psammodromus* and *Gallotia*. Features 22.2 and 39.1 (and possibly 78.1) associate *L. parva* etc. with *Gallotia and Psammodromus*, while absence of inscriptional ribs (30) and nostril separated from first upper labial (if not treated as a character that reverses elsewhere in the assemblage) suggest that *L. parva* and *L. brandtii* are sister species. However these latter features are more homoplasious and the first relationship is preferred.

Lacerta lepida etc., *L. princeps* and the *L. agilis* group

Biochemical evidence (Engelmann and Schäffner, 1981; Lutz and Mayer, 1984) indicates a close relationship between *L. princeps* and *L. lepida*. This presumably also applies to *L. pater*, which has only recently been demonstrated to be specifically distinct from *L. lepida* (Bischoff, 1982). Relationship is also supported by the presence of a derived karyotype in both *L. lepida* and *L. princeps* of 2n = 36, instead of the usual lacertid 2n = 38 (Rykena and Nettman, 1986). The three species also share some derived, although not unique, morphological features including fused postorbital and postfrontal bones in adults (12), frequently very large occipital scale (40.1), prominent blue spots on the flanks and a hemipenial micro-ornamentation of simple hooked spines (78.2).

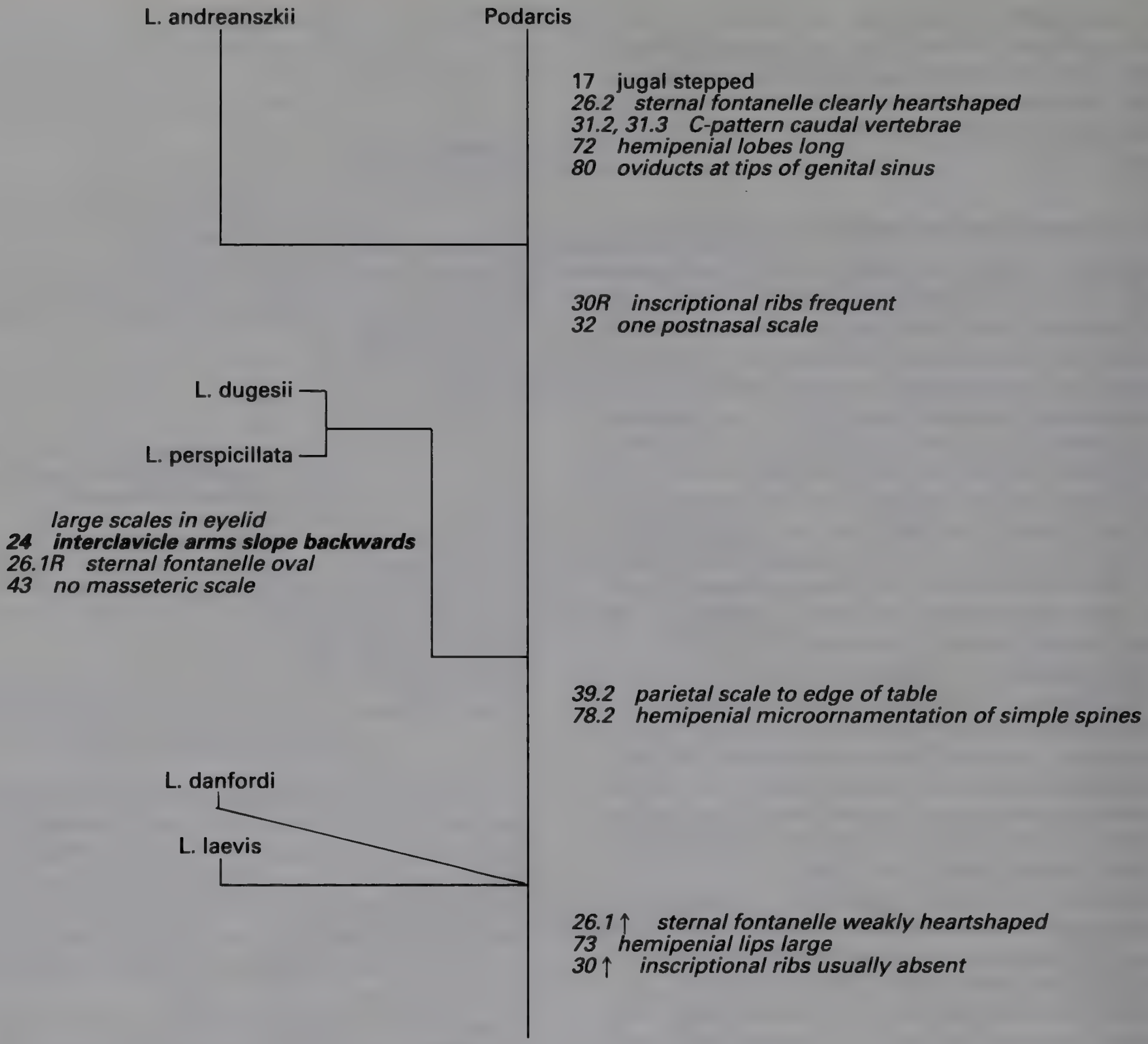

L. andreanszkii
Podarcis
17 jugal stepped
26.2 sternal fontanelle clearly heartshaped
31.2, 31.3 C-pattern caudal vertebrae
72 hemipenial lobes long
80 oviducts at tips of genital sinus
30R inscriptional ribs frequent
32 one postnasal scale
L. dugesii
L. perspicillata
large scales in eyelid
24 interclavicle arms slope backwards
26.1R sternal fontanelle oval
43 no masseteric scale
39.2 parietal scale to edge of table
78.2 hemipenial microornamentation of simple spines
L. danfordi
L. laevis
26.1↑ sternal fontanelle weakly heartshaped
73 hemipenial lips large
30↑ inscriptional ribs usually absent

Fig. 22 Relationships of *Podarcis* and its possible relatives. Characters 31.2, 31.3 and 72 found in *Podarcis* are paralleled in *Lacerta danfordi* etc. For further explanation, see caption of Fig. 20

L. lepida, *L. pater* and *L. princeps* have often been associated with the *Lacerta agilis* group, for instance by Boulenger (1920) and Arnold (1973), but other authors have placed some or all of them close to *Gallotia* (Peters, 1961; Böhme, 1971). In fact, morphological and biochemical evidence does not corroborate this latter view, and albumin immunology and protein electrophoresis (Lutz and Mayer, 1984) suggest that *L. lepida* and its relations are more closely allied to *Podarcis*, the archaeolacertas and *L. graeca* than they are to the *Lacerta agilis* group. However, there is no obvious supporting morphological evidence here either. Instead, a non-unique series of derived features is shared with the *Lacerta agilis* group, including large adult size, usual ossification of the temporal scales (19), no septum on the bodenaponeurosis (82), frequent green dorsal colouring, no bright belly colour and no blue spots on the outer ventral scales (60). *L. lepida* and its two close relatives also share a distinctive growth pattern with the *Lacerta agilis* group in which hatchlings are very 'embryonic' with a very large rounded head and short extremities, and head length shows strong allometric increase in adult males. These growth characteristics do not occur in other large lacertids, such as *Lacerta jayakari* or the species of *Gallotia*. *L. lepida*, *L. princeps* and members of the *L. agilis* group that have been checked all share a similar chromosomal position for the nucleolar organiser (Odierna, Olmo & Cabror, 1987) but, as noted (p. 231), it is not yet clear whether this is a derived feature.

Within the *Lacerta agilis* group, immunology and overall morphological resemblance associate the members of the *L. viridis* assemblage closely (that is all members of the *L. agilis* group except *L. agilis* itself). *L. agilis* lacks the temporal ossification (19) of these forms and has a distinctive high presacral vertebral count (Arnold, 1973) but appears to be their sister taxon. This relationship is supported by a frequent step in the lower border of the outer face of the jugal bone (17) and a tendency for narrow light stripes in the dorsal pattern of some individuals. Another indication of the close affinity of these species is that hybrids between many of them can be produced in captivity (see summaries in Böhme, 1984 and Rudyk, 1986).

L. schreiberi of Spain and Portugal is usually regarded as close to *L. viridis* and electrophoresis appears to support this (J. Mateo, personal communication). It differs in less frequently having a stepped jugal border and in always lacking narrow light stripes, both probably primitive features in which it resembles the *L. lepida*-*L. pater*-*L. princeps* assemblage. Like some members of this, *L. schreiberi* has the postorbital and postfrontal bones regularly fused (12) and is also similar to them in the often fairly large occipital (40.1), the presence of more than six longitudinal rows of ventral scales (48.1), a frequently small preanal scale, and a prominent pattern of light spots, at least laterally, in juveniles. However, all except the first of these features also occur within the *L. viridis* assemblage, in the *L. trilineata* complex (*L. trilineata*, *L. media* and *L. pamphylica*). Furthermore, *L. schreiberi* lacks the distinctive karyotype of *L. lepida* and its relatives, having instead the primitive number (2n = 38) found in *L. viridis* (J. Mateo, personal communication). The position of this species is therefore somewhat equivocal.

***Podarcis* and its likely relatives**

Arnold (1973) pointed out various similarities between *Podarcis* and *Lacerta andreanszkii*, *L. dugesii*, *L. perspicillata*, *L. danfordi* etc and *L. laevis*. It was suggested that *Podarcis* might be most closely related to the first three of these, in particular *L. andreanszkii*. Richter (1980) formalised some relationships using these data, associating *L. perspicillata* and *L. dugesii*, making them the sister group of *Podarcis* s. str. and transferring them to *Podarcis* s. lat. The parsimony consensus tree for primitive Palaearctic and Oriental lacertids associates only *L. perspicillata* and *L. dugesii*, as does compatibility analysis but, as noted, examination of a sample of the more than a hundred alternative trees produced for this assemblage by parsimony analysis shows that the species are frequently associated in the way shown in Fig. 22. Parsimony analysis of just *Podarcis* and these likely relatives produces the same arrangement.

The association of *L. laevis* and *L. danfordi* etc with the rest of the species in Fig. 22 is weak, being based only on the hemipenial lips being large (73), the weakly cordate sternal fontanelle (26.1) and the lack of inscriptional ribs (30). All these reverse subsequently and the last character is widespread elsewhere in the primitive Palaearctic lacertids. *L. danfordi* etc parallels *Podarcis* in two further features, paired transverse processes on the anterior automatic vertebrae (31.2) and long hemipenial lobes (72), which may be some indication of affinity.

Overall relationships among the species of *Podarcis* are difficult to discern from morphology, as the taxa are all very similar in this respect. However, the presence of broad outer sulcal lips on the hemipenial lobes in *Podarcis erhardii* and *P. peloponnesiaca* suggests they are closely related (Arnold, 1973), something which has recently been confirmed by electrophoresis (Mayer, 1986). This technique also demonstrates the affinity of *P. milensis* and *P. gaigiae* (Mayer & Tiedemann, 1980*b*) and immunology indicates the near relationship of *P. filfolensis* and *P. wagleriana* (Lanza & Cei, 1977). The members of each of these species pairs have geographical ranges that are close to one another. A broad immunological study (Lutz & Mayer, 1985) suggests that all these forms plus *P. tiliguerta* and *P. taurica* may be fairly closely related. *P. melisellensis* seems to stand apart on this evidence, although protein electrophoresis and morphology indicate it might be close to *P. taurica*. Immunology, places *P. sicula* and *P. muralis* outside a group constituted by all the foregoing forms. Certainly, a primitive position for *P. muralis* would not be unlikely, as this species, and *P. bocagei* and *P. hispanica*, lack a derived feature of the hemipenis found in all other *Podarcis*, namely attachment of the outer sulcal lips to the walls of the hemipenial lobes so they cannot be reflected (Arnold, 1973).

Archaeolacertas etc. and *Algyroides*

The term archaeolacerta was first used by Méhely (1909) for palaearctic *Lacerta* species in which the skull is depressed and lightly ossified with fenestrated supraocular osteoderms and often no pterygoid teeth; dorsal scales are often flat and smooth and the tail slender and fragile. These features, which vary greatly in their development, appear to be functionally related to the problems of survival in rocky habitats and of using crevices as refuges (Arnold, 1973). Given their apparent lability, these derived morphological characteristics of archaeolacertas, an assemblage which is otherwise generally primitive, do not provide very strong evidence for monophyly, especially as they occur independently in such forms as *Lacerta cyanura*. However, there is biochemical evidence for the affinity of some of the species. Protein electrophoresis associates *L. horvathi*, *L. oxycephala* and *L. graeca* (Mayer and Tiedemann, 1982) while albumin immunology indicates that the first two are related to *L. bedriagae* but separates *L. graeca*, which is as distinct from the others immunologically as they are from *Podarcis* (Lutz and Mayer, 1985). Immunology also indicates that *Lacerta saxicola*, *L. dejugini* and perhaps *L. paraticola* are more closely related to each other than they are to *Lacerta vivipara*, the *Lacerta agilis* group and *Podarcis* (Borisov & Orlova, 1986).

The great interspecific variability of the morphological features of archaeolacertas makes it difficult to define the borders of the group by this means and evidence for membership may conflict. As we have seen *L. graeca* is separated by albumin immunology but the results of protein electrophoresis are nearly identical for this species and *L. oxycephala*. The two also share a derived feature not found elsewhere in the primitive Palaearctic lacertids, namely expanded scales bordering the ventral mid-line of the tail (58), and are also able to hybridise in captivity (Mertens, 1950). Again *L. danfordi* etc has some archaeolacerta features but also similarities to *Podarcis* and its apparent relations

The species regarded as archaeolacertas can be divided into three main groups which may form a sequence. 1. *L. graeca* and *L. oxycephala*, which have the apparently primitive arrangement of two superposed postnasals but expanded subcaudals. 2. More northern and western forms, like *L. mosorensis*, *L. horvathi*, *L. monticola* and *L. bedriagae* in which the postnasal condition appears to be more derived and often variable, some or all individuals having a single postnasal with or without the supranasal contacting the loreal above it, and the rostral often contacting the frontonasal. 3. The *L. saxicola* complex centred in the Caucasus area, the members of which nearly always have a single large postnasal, usually no supranasal-loreal contact and high presacral vertebral counts (commonest numbers: 27 in males, 28 in females). There is evidence that species of this last group have hybridised extensively (Darevskii, 1967), another indicator of close relationship. If the physical features said to characterise archaeolacertas are set aside, they show close resemblance to some other *Lacerta* species found in and around the Caucasus, such as *L. chlorogaster*, *L. derjugini* and *L. praticola*. Most of the resemblance is in primitive characters but these forms share the single postnasal and high presacral vertebral numbers of members of the *L. saxicola* complex and are probably closely related to them. As noted, immunology gives further support in the case of *L. derjugini* and perhaps *L. praticola*.

In general, archaeolacertas are similar to *Podarcis* and its apparent relatives (p. 235) and *Algyroides*. Most of this resemblance is plesiomorphic. They share posterior extension of the parietal scale to the edge of the parietal table of the skull (39.1), but this is also present in the *L. parva-Psammodromus-Gallotia* assemblage. However, immunology suggests *Podarcis* and some archaeolacertas are quite closely related (Lutz and Mayer, 1984; Lutz, Bischoff and Mayer, 1986). There is nevertheless, no evidence for the idea that archaeolacertas were derived polyphyletically from within *Podarcis*, as suggested by Boulenger (1920) and Klemmer (1957).

L. jayakari etc, *L. cappadocica*, *L. vivipara* and *Takydromus*

Parsimony and compatibility treatments confirm the association of *L. jayakari* etc. with the Ethiopian and advanced Saharo-Eurasian clade. No other taxon is consistently and directly associated with these forms but, in many of the alternative parsimony trees produced when the primitive Palaearctic and Oriental lacertids were analysed, *Takydromus* etc., *Lacerta cappadocica* and *L. vivipara* were often connected to them. Parsimony analysis restricted to all the foregoing taxa produces five alternative trees with a consistency of 0.795, all again making *Lacerta jayakari* and the Ethiopian and advanced clade sister groups, but associating these and the other taxa in a variety of ways.

As noted by Boulenger (1921) the primitive members of the distinctive East Asian genus *Takydromus* have considerable similarity to *Lacerta vivipara*. *Takydromus* etc. shares more states with this species than with any other taxon, although these vary in their development and consistency and none is unique (Table 1). This resemblance is not emphasised in parsimony analysis because some of the characters concerned are variable within one or both taxa, being consequently scored as 0 rather than 1 (see p. 229), and so do not contribute to assessments of relationship. In some parsimony treatments, *L. vivipara* is often associated with *L. andreanszkyi*, the two sharing characters 32, 35, 39.1, 39.2 and 60. But, resemblance to *Takydromus* etc. in derived features is greater and may indicate a real relationship.

If the polarity of some characters, where the evidence for the primitive state conflicts, is changed (run 4, p. 231), *Takydromus* etc. is associated with *L. cappadocica* and sometimes *L. vivipara* in a proportion of the alternative trees produced by parsimony methods. However, as already noted, the trees concerned have more steps than those where polarities are unaltered.

General relationships

As already seen, the affinities of taxa within the groups discussed above are often equivocal and this is even more marked when overall relationships among primitive Palaearctic lacertids are considered. Neither parsimony nor compatibility treatments of morphological data give a detailed and consistent pattern of relationships but, when original polarities are used, trees produced by parsimony often have two main branches. One of these includes *Takydromus* etc., *L. cappadocica*, *L. jayakari* etc. and the African and advanced Saharo-Eurasian clade, *L. lepida* and *L. princeps*, the *L. agilis* group and often *L. vivipara* as well; the other branch includes everything else. The arrangement is also frequent with some polarity modifications (runs 2 and 3, p. 231). However, evidence for the reality of the two branches is weak, the first being supported consistently only by character 60 and the second by 39.1. Also, relationships within the two assemblages show great variation. This general pattern is shown in Fig. 23.

Table 1 Apparent synapomorphies of *Takydromus* and *Lacerta vivipara*

	Takydromus	*Lacerta vivipara*
Anterior descending processes of frontal bone reduced (6.1)	+	often
Postorbital and postfrontal bones fused (12)	+	+
Loop of clavicle continuous (22.2)	+	most cases
A pattern caudal vertebrae (31.1)	+	+
Single postnasal scale (32)	usual	+
Supranasal and loreal scales often in contact (35)	+	+
Parietal scale to edge of parietal table (39.2)	often	+
Femoral pore row reduced (51.1)	+	sometimes
Retractor lateralis anterior broad in front of vent, often joining its anterior lip (67)	+	+
Hemipenial sheath very weak	+	+

In an attempt to clarify relationships among the western Palaearctic lacertid groups, comparative albumin immunology has been carried out on *L. cappadocica*, *L. jayakari*, *L. vivipara*, *L. bedriagae*, *L. graeca*, *Podarcis*, members of the *L. agilis* group, *Psammodromus* and *Gallotia* (Lutz & Mayer, 1985; Lutz, Mayer & Bischoff, 1986). These studies associate *L. cappadocica* with *L. graeca*, *L, bedriagae* and *Podarcis*, while *L. jayakari* may be connected here or just possibly with the *L. agilis* group. In one study, there is no indication of a very close connection of any of these forms with *Lacerta vivipara* (Lutz, Bischoff & Mayer, 1986) but it is associated with the *L. agilis* group in the other (Lutz & Mayer, 1985). All these forms are immunologically closer to each other than they are to *Psammodromus* and *Gallotia*.

It is apparent from the foregoing discussion that the higher relationships of primitive Palaearctic lacertids are by no means clear. Morphological data does not give an unequivocal pattern and differs considerably from that derived from immunology. The latter is incomplete in its coverage and some of the data is open to different interpretations (Busack & Maxson, 1987). Biochemical and karyological data must be more comprehensive and additional sources of evidence, such as DNA sequencing, need to be investigated if relationships are to be elucidated. However, if the main branching events in the phylogeny occurred swiftly, without much evolutionary change between dichotomies, comprehensive reconstruction of the cladogenetic history of primitive Palaearctic and Oriental lacertids may not be possible.

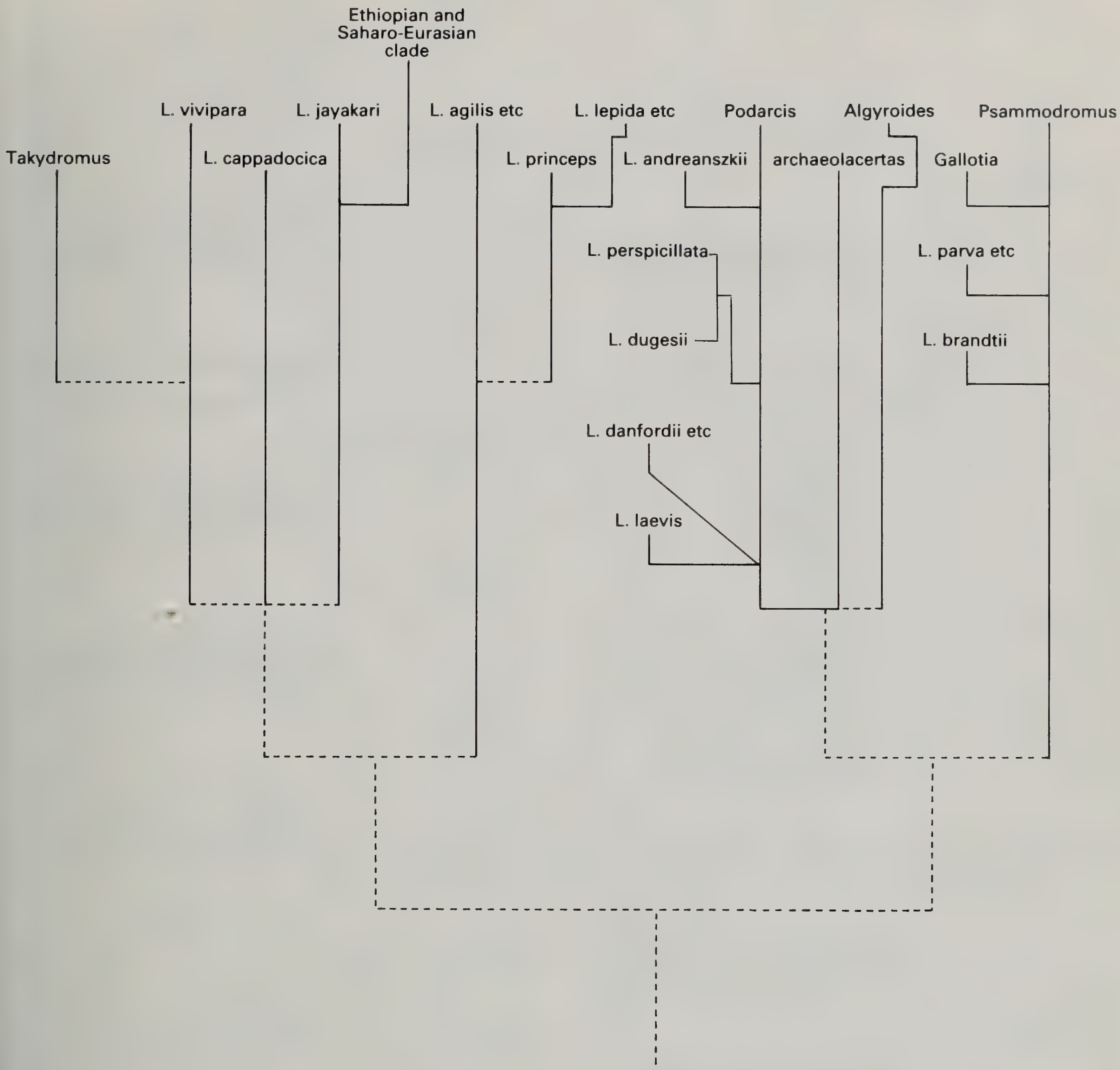

Ethiopian and Saharo-Eurasian clade
L. vivipara
L. jayakari
L. agilis etc
L. lepida etc
Podarcis
Algyroides
Psammodromus
Takydromus
L. cappadocica
L. princeps
L. andreanszkii
archaeolacertas
Gallotia
L. perspicillata
L. parva etc
L. dugesii
L. brandtii
L. danfordii etc
L. laevis

Fig. 23 Putative relationships of primitive Palaearctic lacertids based mainly on morphology. Interrupted lines indicate the more tentative associations. Albumin immunology separates *Gallotia* and *Psammodromus* from the rest.

ETHIOPIAN AND ADVANCED SAHARO-EURASIAN FORMS

Parsimony analysis

Characters which have no shared derived states within the group made up of *Lacerta jayakari* etc. and the Ethiopian and advanced Saharo-Eurasian forms were eliminated. In addition to those listed on p. 229, these were 17, 18, 22.1, 24, 25, 35, 38, 43, 51.1, 58, 67, 70, 72, 73, 77, 78.1, 81.1, 82, 83, and 84, reducing the data set to 78 characters. Parsimony analysis was then carried out, resulting in four alternative trees of 196 steps and a consistency index of 0.398. These trees are not much different from the relevant section of the consensus tree for the whole Lacertidae and very similar to the estimate of phylogeny finally preferred (Fig. 24). Most taxa are arranged along a single stem with a separate branch near the base containing *Adolfus africanus* etc., *A. alleni*, *Bedriagaia*, *Gastropholis*, *Holaspis*, *'Lacerta' echinata* and *L. jacksoni*, which will be referred to as the Equatorial African clade. On the main stem, *Philochortus* and its more derived relatives, lying above it on the tree, form a distinct group specified by a relatively large number of synapomorphies. Most of the tree topology is constant, but *Pedioplanis* and *Eremias* appear either as successive branches or as sister groups, and within

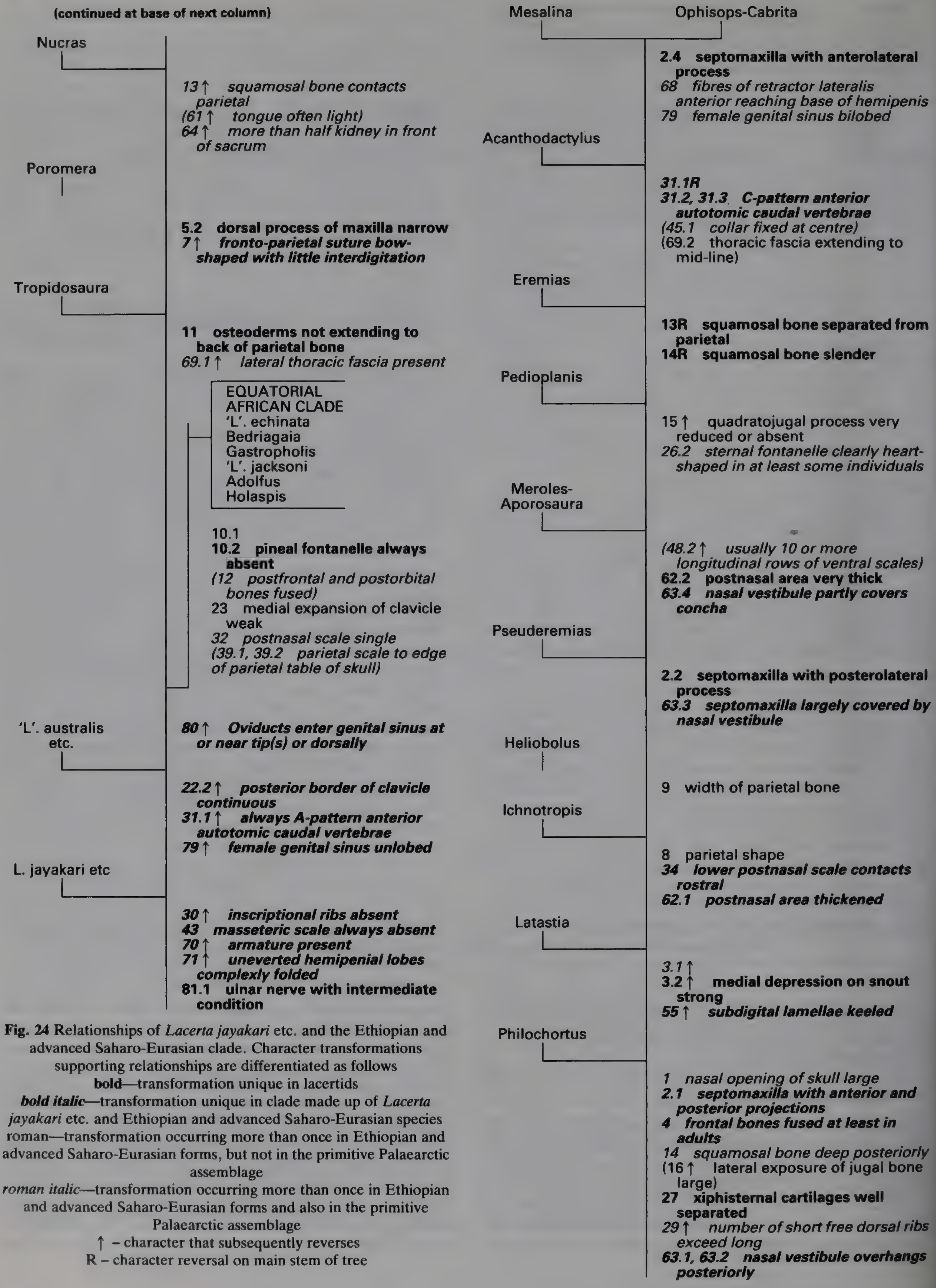

(continued at base of next column)
Nucras
13↑ squamosal bone contacts parietal
(61↑ tongue often light)
64↑ more than half kidney in front of sacrum
Poromera
5.2 dorsal process of maxilla narrow
7↑ fronto-parietal suture bow-shaped with little interdigitation
Tropidosaura
11 osteoderms not extending to back of parietal bone
69.1↑ lateral thoracic fascia present
EQUATORIAL AFRICAN CLADE
'L'. echinata
Bedriagaia
Gastropholis
'L'. jacksoni
Adolfus
Holaspis
10.1
10.2 pineal fontanelle always absent
(12 postfrontal and postorbital bones fused)
23 medial expansion of clavicle weak
32 postnasal scale single
(39.1, 39.2 parietal scale to edge of parietal table of skull)
'L'. australis etc.
80↑ Oviducts enter genital sinus at or near tip(s) or dorsally
22.2↑ posterior border of clavicle continuous
31.1↑ always A-pattern anterior autotomic caudal vertebrae
79↑ female genital sinus unlobed
L. jayakari etc
30↑ inscriptional ribs absent
43 masseteric scale always absent
70↑ armature present
71↑ uneverted hemipenial lobes complexly folded
81.1 ulnar nerve with intermediate condition
Mesalina
Ophisops-Cabrita
2.4 septomaxilla with anterolateral process
68 fibres of retractor lateralis anterior reaching base of hemipenis
79 female genital sinus bilobed
Acanthodactylus
31.1R
31.2, 31.3 C-pattern anterior autotomic caudal vertebrae
(45.1 collar fixed at centre)
(69.2 thoracic fascia extending to mid-line)
Eremias
13R squamosal bone separated from parietal
14R squamosal bone slender
Pedioplanis
15↑ quadratojugal process very reduced or absent
26.2 sternal fontanelle clearly heart-shaped in at least some individuals
Meroles-Aporosaura
(48.2↑ usually 10 or more longitudinal rows of ventral scales)
62.2 postnasal area very thick
63.4 nasal vestibule partly covers concha
Pseuderemias
2.2 septomaxilla with posterolateral process
63.3 septomaxilla largely covered by nasal vestibule
Heliobolus
9 width of parietal bone
Ichnotropis
8 parietal shape
34 lower postnasal scale contacts rostral
62.1 postnasal area thickened
Latastia
3.1↑
3.2↑ medial depression on snout strong
55↑ subdigital lamellae keeled
Philochortus
1 nasal opening of skull large
2.1 septomaxilla with anterior and posterior projections
4 frontal bones fused at least in adults
14 squamosal bone deep posteriorly
(16↑ lateral exposure of jugal bone large)
27 xiphisternal cartilages well separated
29↑ number of short free dorsal ribs exceed long
63.1, 63.2 nasal vestibule overhangs posteriorly

Fig. 24 Relationships of *Lacerta jayakari* etc. and the Ethiopian and advanced Saharo-Eurasian clade. Character transformations supporting relationships are differentiated as follows
bold—transformation unique in lacertids
bold italic—transformation unique in clade made up of *Lacerta jayakari* etc. and Ethiopian and advanced Saharo-Eurasian species
roman—transformation occurring more than once in Ethiopian and advanced Saharo-Eurasian forms, but not in the primitive Palaearctic assemblage
roman italic—transformation occurring more than once in Ethiopian and advanced Saharo-Eurasian forms and also in the primitive Palaearctic assemblage
↑ – character that subsequently reverses
R – character reversal on main stem of tree

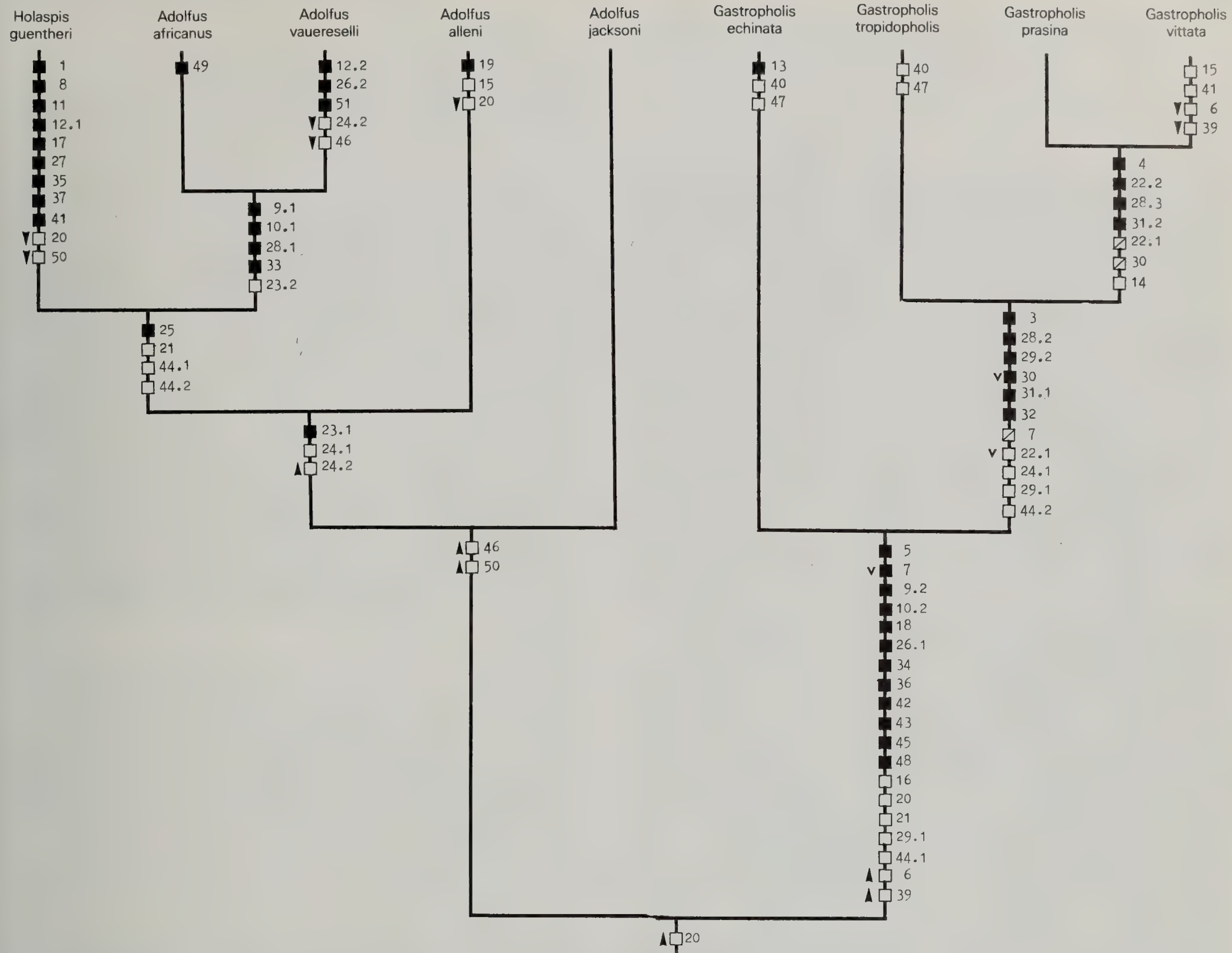

Holaspis guentheri
Adolfus africanus
Adolfus vauereselli
Adolfus alleni
Adolfus jacksoni
Gastropholis echinata
Gastropholis tropidopholis
Gastropholis prasina
Gastropholis vittata
1
8
11
12.1
17
27
35
37
41
20
50
49
12.2
26.2
51
24.2
46
19
15
20
13
40
47
40
47
15
41
6
39
4
22.2
28.3
31.2
22.1
30
14
9.1
10.1
28.1
33
23.2
25
21
44.1
44.2
3
28.2
29.2
V
30
31.1
32
7
V
22.1
24.1
29.1
44.2
23.1
24.1
24.2
46
50
5
V
7
9.2
10.2
18
26.1
34
36
42
43
45
48
16
20
21
29.1
44.1
6
39
20

Fig. 25 Relationships of Equatorial African clade. Solid symbols indicate unique transformations within the clade, and open symbols those that occur twice. Upward pointers denote characters that subsequently reverse, at which point they are marked by downward pointers. Characters that are variable but later stabilise are indicated by V. Figures refer to specific characters; for details see Arnold, 1989.

the Equatorial African clade, the relationships of the unit made up of *Lacerta echinata*, *Bedriagaia* and *Gastropholis* to *Adolfus africanus etc*. and *Adolfus alleni* are variable.

As there are some parallelisms between the Equatorial African clade and the main branch, all the species of the former, except the most primitive, *'L'. jacksoni*, were excluded, and characters which consequently had no shared derived states eliminated, namely 19, 22.2, 23, 42, 49.1, 49.2, 52, 59, 74. Parsimony analysis now produced just two trees of 146 steps and a consistency index of 0.473, but the ambiguity in the relationship of *Pedioplanis* and *Eremias* remained. *Philochortus* and its advanced relatives were also analysed separately in an attempt to resolve this problem, being run by the 'Branch and Bound' method. Additional characters without shared derived states eliminated were 1, 2.1, 4, 5.2, 7, 10.2, 11, 26.3, 27, 29, 30, 32, 45.2, 47, 54.2, 60, 63.1, 63.2, 64, 71, 75 and 81.2, reducing the data set to 48 characters. This again produced two trees, of 96 steps and a consistency of 0.5, with the same variants.

Compatibility analysis

Data for *Lacerta jayakari* etc. and the Ethiopian and advanced Saharo-Eurasian forms were reanalysed by the compatibility method. This gave an overall randomness ratio of 0.83 and a compatible set of 24 characters resulting in the tree shown in fig. 19 b. Resolution is increased and the arrangement of taxa changed somewhat from that in Fig. 19 a. In general, the result is similar to the one produced by parsimony analysis, but with less definition. Removal of most members of the Equatorial clade and of *L. jayakari* etc., produces very little change. When the robust assemblage made up of *Philochortus* and its derived relatives are analysed separately, the randomness ratio is 1.01 and the *Eremias-Pedioplanis* anomaly is resolved, with *Pedioplanis* and *Eremias* being successive banches of the tree (Fig. 19c).

The Equatorial African clade

Both parsimony and compatibility methods discern *Gastropholis* and *Bedriagaia* as sister taxa and recognise *'Lacerta' echinata* as their nearest relative. Consideration of a larger data set for the Equatorial African clade (Arnold, 1989) confirms this grouping and produces a general pattern of relationships (Fig. 25).

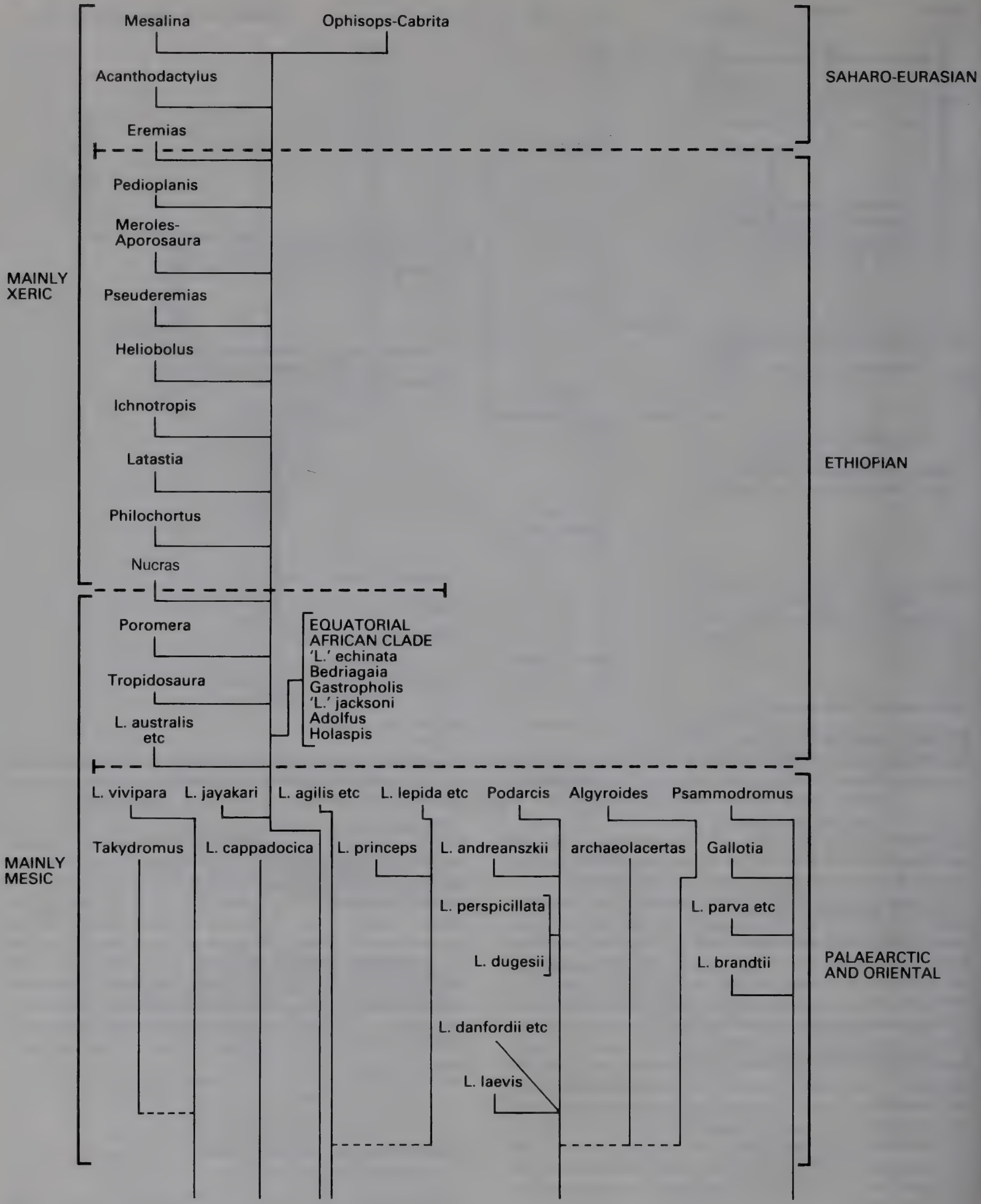

Mesalina
Ophisops-Cabrita
Acanthodactylus
Eremias
Pedioplanis
Meroles-Aporosaura
Pseuderemias
Heliobolus
Ichnotropis
Latastia
Philochortus
Nucras
Poromera
Tropidosaura
L. australis etc
EQUATORIAL AFRICAN CLADE
'L.' echinata
Bedriagaia
Gastropholis
'L.' jacksoni
Adolfus
Holaspis
L. vivipara
L. jayakari
L. agilis etc
L. lepida etc
Podarcis
Algyroides
Psammodromus
Takydromus
L. cappadocica
L. princeps
L. andreanszkii
archaeolacertas
Gallotia
L. perspicillata
L. dugesii
L. parva etc
L. brandtii
L. danfordii etc
L. laevis
MAINLY XERIC
MAINLY MESIC
SAHARO-EURASIAN
ETHIOPIAN
PALAEARCTIC AND ORIENTAL

Fig. 26 Principal ecological and zoogeographic trends in the Lacertidae. Advanced taxa occur in mainly xeric habitats, while more primitive forms usually occupy quite mesic situations. The most primitive taxa are found in the Palaearctic and Oriental regions, with a group of increasingly advanced forms occupying the Ethiopian region and the most advanced occurring in the Saharan area and in the drier parts of Eurasia.

Areas of conflict

The preferred relationships of *Lacerta jayakari*, the Ethiopian species and the advanced Saharo-Eurasian forms is shown in Fig. 24. Sections where parsimony and compatibility methods differ in results or degree of resolution are discussed below.

Tropidosaura and *Poromera*.

Parsimony joins these genera as sister groups on the basis of three features involving five characters: loss of anterior frontal processes (6.1, 6.2), reduced collar (45.1, 45.2) and enlarged dorsal body scales (46). Against this, compatibility methods relate *Poromera* to more advanced forms on the strength of the dorsal process of the maxilla (5); another slightly less constant feature that also supports this relationship is the form of the fronto-parietal suture (7). Although less features support the second arrangement than the first, they are considerably less homoplasious within the Lacertidae as a whole and consequently likely to be better indicators of relationship. Given this conflict between greater number of characters on one side and perhaps better quality characters on the other, it seems best to leave the detailed relationship of *Tropidosaura* and *Poromera* unresolved.

Ichnotropis and *Heliobolus*.

Parsimony also joins these two genera as sister groups on the basis of two features and three characters: loss of anterior frontal processes (6.1, 6.2) and kidney not extending far beyond vent (65). In contrast, compatibility associates *Heliobolus* with more advanced forms on parietal width (9), although this feature also occurs in some presumably derived *Ichnotropis*. The first arrangement is supported by two instead of one binary character, but these are more homoplasious than the latter. Because of this, the relationship of *Ichnotropis* and *Heliobolus* is left undetermined.

Pedioplanis and *Eremias*.

As noted, these two genera may appear in parsimony analysis as sister groups, or *Eremias* may be associated with more advanced forms. Sister group relationship is based on large jugal exposure (16), parietal scale reaching the edge of the parietal table of skull (39.1, 39.2) and bilobed female genital sinus (79). These characters are all quite noisy, showing considerable homoplasy in the rest of the Lacertidae, and 16 and 79 are also reversals. Features associating *Eremias* with more advanced taxa than *Pedioplanis* are squamosal-parietal separation (13), shape of squamosal (14), number of chin shields (44) and hemipenial micro-ornamentation (78.2). All these are reversals, and 44 and 78.2 have numerous homoplasies elsewhere in the Lacertidae, but 13 and 14 have none. These latter two characters perform better in 'boil down' than the set supporting sister group relationship, when all Ethiopian and advanced Saharo-Eurasian forms are considered, and appear in the compatible set when just *Philochortus* and its advanced relatives are subjected to compatibility analysis. Given the greater apparent stability of characters 13 and 14, the relationship they support is preferred here.

BIOGEOGRAPHICAL ASPECTS OF LACERTID PHYLOGENY

The general pattern

The phylogeny proposed here exhibits broad geographical regularity (fig. 26). 1. The most primitive lacertid genera are found in relatively mesic habitats in the Palaearctic and Oriental regions, where the majority are restricted to the west. 2. A series of increasingly more advanced forms occupies the Ethiopian region (i.e. Africa south of the Sahara, also called the Afrotropical or Africotropical—Udvardy, 1975) with the more derived occurring in arid situations. 3. Finally, *Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops-Cabrita*, which originated from the latter, occur in and around the deserts of the North Africa and Eurasia, and in the Indian subcontinent. A simple explanation of this pattern would be that modern lacertids arose in Eurasia, invaded Africa and the Ethiopian region, evolved more xeric forms in the latter area, and then one or more derivatives of these re-entered the dry areas of Eurasia and North Africa and radiated.

The presence of the majority of the generally primitive lacertids, and indeed the most primitive modern forms, in Europe indicates the family may well have originated there, which is also supported by their long, if fragmentary, fossil history in the area, extending back at least as far as the Palaeocene (Estes, 1983*a*). Albumin immunology suggests that the ancestors of many modern western Palaearctic lacertids may have undergone quite rapid multiple divergence, perhaps during the early Miocene, a time when the European land-mass was very dissected, something which would have facilitated differentiation (Lutz, Bischoff & Mayer, 1986). The immunological information implies that *Lacerta jayakari* may have separated from the other Palaearctic lacertids investigated about 17-20 million years ago. This species, together with its close relative, *L. cyanura*, appears to be the sister group of the whole Ethiopian and advanced Saharo-Eurasian clade so, if the immunological date is accepted, the latter very large and diverse assemblage must have originated subsequently.

Representitives of a number of separate lacertid stocks occur in Africa and the associated Arabian area, including *Lacerta lepida* etc., members of the *Psammodromus-Gallotia* assemblage, some species of *Podarcis* and its apparent relatives, *L. jayakari* etc. and, of course, the associated Ethiopian and advanced Saharo-Eurasian clade. All except the last unit are presently confined to the northern, Palaearctic periphery of the African-Arabian plate. The times of arrival of these various groups is unknown, but it should have been possible for lacertids to reach the area easily from some time around the closure of the Tethys sea which previously separated it from Eurasia. The date for the principle closure is estimated to be mid-Burdigalian, around 17 million years ago, when Arabia contacted the Turkish plate. Temporary connexion may also have occurred earlier in the Aquitanian (Adams, Gentry & Whybrow, 1983; Whybrow, 1984) and there may have been a brief interruption of land contact during the Langhian transgression around 16 milllion years ago (Steininger, Rabeder & Rögl, 1985). The Burdigalian was a time of faunal interchange among mammals between Eurasia and Africa. By the middle of this stage, proboscideans and creodonts of African origin were in Europe and Eurasian carnivores in Africa (Steininger, Rabeder & Rögl, 1985). Among reptiles, a representitive of the apparently African chameleons had reached central Europe by the Ottnangian (= upper Burdigalian) (Roček, 1984), so some lacertids might have entered Africa by then. The immunological date for the separation of *Lacerta jayakari* and consequently of the Ethiopian clade fits rather well with this. Any lacertids entering Africa through most of the Miocene are likely to have arrived via Arabia, for the proximity of Africa and Europe at the western end of the Mediterranean did not occur until the end of this period. Interestingly, the range of *L. jayakari* etc is the closest of any members of the primitive Palaearctic lacertids to the Ethiopian region by this route. Whenever the ancestors of Ethiopian lacertids entered Africa, the date when advanced xeric forms derived from them spread north into the arid regions of Eurasia and Northern Africa must inevitably have been considerably later.

Estes (1983*b*) suggested that the lacertids may have arisen on one of the islands that constituted Europe during the Jurassic, undergoing vicariance from a North American stock which was ancestral to teiid lizards. Presumably, these early lacertids would have given rise to the ones that appear to have existed in the European area throughout the Cenozoic. Estes thought that the more advanced African forms might have differentiated from the European ones on the island that constituted Northwest Africa in the Cretaceous. But, as we have seen, immunology suggests a much later date for the origin of the Ethiopian and advanced Saharo-Eurasian clade, and also for some groups that now occur in North Africa. An alternative version of events discussed by this author is that lacertoids were a Gondwanaland element which split into lacertid and teiid precursors with the separation of Africa and South America in the Cretaceous period. Presumably this would have been followed by Europe being invaded by primitive forms, which have persisted with relatively little change until the present day, and by such forms becoming extinct in Africa.

The various hypotheses that have been proposed for the gross historical biogeography of the Lacertidae are open to testing. Evolutionary clocks, based on immunology, amino-acid substitution in proteins or base substitution in DNA, may give a better idea of when the Ethiopian and advanced Saharo-Eurasian clade arose and when the xeric Saharo-Eurasian section of this separated. Regrettably, there is as yet no lacertid fossil record known in Africa south of the Sahara and virtually no material from the north of the continent either (Estes, 1983*a*), but discovery of suitable deposits may throw light on possible dates of arrival. Whether, the invasion of more northern areas by advanced xeric forms was indeed a relatively late event might also be tested by fossil evidence.

Primitive Palaearctic and Oriental forms

It is not possible to work out the overall historical biogeography of this assemblage, partly because the phylogeny is incomplete in some areas and uncertain in others. As noted, the majority of primitive lacertids are restricted to the west Palaearctic. However, one *Lacerta*, *L. vivipara*, extends eastwards to the Pacific Ocean and *Takydromus* etc. is found only in the east Palaearctic and the Oriental regions. It is not possible to be sure how the almost entirely allopatric range of *Takydromus* etc. arose. If it is indeed a derivative of the paraphyletic genus *Lacerta*, its origins may lie in the European region, either its *Lacerta* ancestor migrating eastwards from this area or *Takydromus* actually evolving there. *Miolacerta* Roček, 1984, from the lower Miocene (Ottnangian) of Czechoslovakia, has tridentate lateral teeth, like *Takydromus* etc., but whether this is indicative of relationship is unknown.

A striking aspect of the distributional pattern of primitive lacertids in the western Palaearctic is the way archaeolacertas have very limited and disjunct ranges in Europe west of the Black Sea, although they are more widely distributed in Asiatic Turkey, the Caucasus and adjoining areas. In the west, they are largely restricted to high mountain massifs and it seems possible that the distributional patterns of these forms may have arisen through competition with similarly sized members of *Podarcis* which occur widely over southern Europe but not further east (Arnold, 1981b). *Podarcis* may also have restricted *Algyroides*, which again has a broken and small distribution.

Three apparent clades of primitive Palaearctic lacertids have a disjunct distribution with taxa both in southwest Asia (especially Turkey, north Iraq, northwest Iran and the Eastern seaboard of the Mediterranean) and in northwest Africa, the latter sometimes with representatives in Iberia, the Canary Islands or Madeira (Table 2). As will be seen, the same general pattern occurs in a number of other reptile taxa. Differentiation between eastern and western representatives is often very variable. In some cases forms are conspecific and disjunction may be due to recent aridification in North Africa. But in other instances, like the primitive lacertids, eastern and western sections are much more distinct and the differentiation is probably much longer standing.

Table 2 The members of some apparent clades of reptiles found in Southwest Asia and Northwest Africa

Southwest Asia	Northwest Africa etc.
Primitive Palaearctic lacertids	
1. *Lacerta brandtii*, *L. parva* etc	*Psammodromus*, *Gallotia*
2. *Lacerta danfordi* etc., *L. laevis*	*Lacerta andreanszkyi*, *L. dugesii*, *L. perspicillata* primitive *Podarcis*
3. *Lacerta princeps*	*Lacerta lepida* etc.
Other groups	
4. *Acanthodactylus tristrami* etc.	*Acanthodactylus erythrurus* etc.
5. *Ophisaurus apodus*	*Ophisaurus koellikeri*
6. *Blanus strauchi*	*Blanus cinereus*
7. *Vipera lebetina* subspp.	*Vipera mauretanica* etc.
8. *Mauremys caspica*	*Mauremys leprosa*
9. *Testudo g. ibera*	*Testudo g. graeca*

Ethiopian forms

In Africa, the more primitive forms of the Ethiopian and advanced Saharo-Eurasian clade appear to have spread widely, for the apparently most basal section, *'Lacerta'*

Table 3 Distribution of non-mesic groups of lacertids and their primitive forms in the Ethiopian region

	Distribution of group	Distribution of primitive forms
Nucras	Widespread, south of equatorial forest	Equatorial east
Philochortus	Northeast, also southern edge of Sahara with relicts further north	Northeast
Latastia	Northeast and east, savannah south of Sahara	Northeast
Heliobolus	Widespread, south of equatorial forest, also savannah north of forest	North
Ichnotropis	Widespread, south of equatorial forest	Equatorial east
Pseuderemias	Northeast	Northeast
Meroles	Southwest	Southwest
Pedioplanis	South	South

australis etc, occurs in the far south of the continent. Penetration southwards into the Ethiopian region and broad dispersal there would have been easy before the later Neogene, while conditions were widely mesic in Africa (Axelrod & Raven, 1978). In general, primitive Ethiopian taxa now have disjunct ranges, being confined to less dry areas, with *L. australis* etc. and *Tropidosaura* in various often isolated montane areas of southern Africa and *Adolfus*, *Gastropholis*, *Holaspis* and *Poromera* in the Equatorial forest region. *Nucras* and more advanced Ethiopian generic units form a sequence that occupies generally increasingly severe habitats in which aridity, high temperature and openess become more marked. This evolution may have been related to the increasing dryness of the African climate during the later Neogene (Axelrod & Raven, 1978).

Among these relatively xeric genera, most are found in the northeast and north of the drier parts of the Ethiopian region, or have their most primitive representatives there if they extend southwards (Table 3). Perhaps, this is the area where they each originated, or is at least ecologically similar. A couple of genera, *Latastia* and *Heliobolus* extend to the southern periphery of the dry areas of northern Africa and one species of *Philochortus* is more widespread there, albeit with a relict distribution. The only exceptions to the general pattern are the most advanced Ethiopian genera, *Meroles-Aporosaura* and *Pedioplanis*, which are now entirely confined to arid parts of southern Africa. However, these areas may well have been connected in the past with the dry northeast of the Ethiopian region (Balinsky, 1962; Seely, 1978), where *Pseuderemias*, the closest Ethiopian relative of *Meroles-Aporosaura* and *Pedioplanis*, is found; so these genera too may have had a northern origin. It is also possible that the precursor of advanced Saharan and Eurasian lacertids, to which *Pedioplanis* appears to be the sister group, evolved somewhere in the northern parts of the Ethiopian region.

Advanced North African and Eurasian forms

These occur mainly in dry habitats and cover an immense geographical area. Although there are only four genera, the group is very speciose with a total of about 69 species, of which 61 are members of *Eremias*, *Acanthodactylus* and *Mesalina*. This compares with 54 species distributed among eight genera in the Ethiopian xeric forms. Possibly, once advanced dry-adapted lacertids arose in the Ethiopian region, they were able to enter unoccupied niche space in the Saharo-Sindian and associated central Asian desert areas, including their peripheries, and radiate there. Certainly, the dry regions where they are found do not have many other lizards that are diurnal and arid-adapted, with high heat tolerance and active hunting strategies. It is of course possible that these advanced lacertids have displaced other forms. Perhaps primitive Palaearctic taxa with some adaptation to arid conditions, such as *Psammodromus* were once more widespread and the same may have been true of genera of Ethiopian origin that now occur only on the southern edge of the North African arid regions such as *Latastia* and *Heliobolus*, but there is no evidence of this in the form of fossils or isolated relict populations.

Although originally adapted to dry conditions, some members of the advanced Saharo-Eurasian clade show a tendency to enter rather more mesic habitats. This is especially true of *Ophisops-Cabrita* which does not penetrate into very dry areas, but the trend is also apparent in the *erythrurus* and *guineensis* species groups of *Acanthodactylus* in northwest and west Africa and, to a lesser extent, probably in sections of *Eremias* and *Mesalina* in Asia as well.

Advanced Saharo-Eurasian lacertids show some vicariance. *Eremias* is essentially confined to the Palaearctic deserts of central Asia and its environs, while the ecologically similar *Acanthodactylus*, and *Mesalina* occur mainly further south in Asia and into North Africa. As noted, *Ophisops-Cabrita* is the only generic group of lacertids to extend far into the Indian subcontinent.

One striking aspect of the distribution of advanced Saharo-Eurasian lacertids is that, although the arid region of North Africa is a very large part of their total range, it has a relatively sparse representation of these forms, in terms of species numbers. There are only fifteen endemic species present plus five more that also occur further east. This compares with about 23 in the much smaller Arabian subregion and a total of 49 species in southwest and central Asia as a whole. Of the four genera one, *Eremias*, is entirely confined to Eurasia and, in *Acanthodactylus* and *Ophisops-Cabrita*, not only many more species occur in the east, but also more of the main branches of the phylogenies of these groups. Although less marked, this is also true of *Mesalina*.

The pattern is not restricted to lacertids, being repeated in a number of other reptile groups, including *Agama (Trapelus)*, *Uromastyx*, *Stenodactylus*, *Scincus*, and *Lytorhynchus*. These forms make up a very substantial proportion of the Saharan herpetofauna and the number of taxa that have species in the Sahara but not further east is small, the main groups being *Scincopus*, *Sphenops* and some species of *Tarentola*. In these cases, the desert forms appear to be derived from stocks in adjoining more mesic areas of Africa, respectively the *Eumeces schneideri* group, *Chalcides* and more primitive members of *Tarentola*. The low level of endemicity found in the Sahara suggests that, although it is by far the largest desert in the world at the present time, most stocks occuring there now have had a longer continuous history in the east. Possibly, but by no means certainly, Asia was colonised by advanced lacertids before northern Africa. A land-bridge existed between the Horn of Africa and southern Arabia until the early Pliocene, which would have made this possible, and direct connection between Arabia and North Africa developed soon after it was interrupted (Whybrow, 1984). The relationships of the Saharan reptile fauna will be discussed more fully elsewhere.

MAIN ECOLOGICAL AND MORPHOLOGICAL TRENDS IN LACERTID PHYLOGENY

Shift from mesic to xeric habitats

The most obvious trend in lacertid phylogeny is a shift from mesic habitats to increasingly more xeric ones (Fig. 26). This is weakly apparent in the *Gallotia-Psammodromus* lineage among the primitive Palaearctic forms and more obviously so in the Ethiopian and advanced Saharo-Eurasian clade. Here, *Nucras* and all its more derived relatives occur in relatively dry habitats.

Although a detailed case has not yet been made, many of the morphological changes that occur in advanced forms may well be functionally associated with the problems of survival in dry, hot environments that are often very open. A number of changes affect the snout and nasal region and could be connected with processing dry, often dusty air. Possibilities here include the large nasal opening of the skull (1), complex septomaxilla (2.1–2.4), median depression on snout (3.1–3.2), lower postnasal contacting the rostral (34), thickened postnasal area (62.1–62.2) and often complex nasal passage (63.1–63.4). The increase in the extent of the anterior kidney (64) may be related to reduction in available water, and keeled subdigital lamellae (55) appear to be important in reducing heat uptake from the ground (Arnold, 1973).

Open habitats presumably increase viewing distances which is likely to place a premium on visual acuity and be responsible for the development of the large eyes typical of these advanced forms. This in turn results in narrowing of the frontal area, perhaps making it less strong, and the fusion of the frontal bones (4) may counteract this. The more complex frontal interdigitation with the bones of the snout (5) could also increase strength. The general lightening of the skull in advanced forms, such as the reduction in osteoderms (11), may again be connected with open habitats, which might be responsible for postcranial changes as well, in particular shift from generally long, sinuous bodies with short limbs to shorter torsoes with longer legs. Perhaps associated with this is the remodelling of the thoracic region, with more widely separated xiphisternal cartilages (27), and increase in the number of short dorsal ribs (29). Another series of changes involves the back of the head, including a simpler fronto-parietal suture (7), shorter posterior cranial segment (8, 9) and loss of the quadratojugal process, perhaps all connected with greater skull mobility.

Parallelism in ecological niche and its role in character homoplasy

As might be expected in a family with a very large range, quite different lineages have entered very similar niches in different places. This has resulted in considerable character parallelism, since similar morphological adaptations are often elicited. For instance, habitual use of narrow crevices, particularly in rocks, occurs in some archaeolacertas, *Podarcis*, *L. cyanura* and *Holaspis* and produces a whole suite of characters (Arnold, 1973). Forms adapted to forest floor and forest edge habitats occur in *Adolfus*, *Algyroides* and among primitive *Takydromus*, while other *Takydromus* and *Poromera* specialise in climbing and running through long grassy vegetation, producing parallels in such features as elongate, slender habitus, enlarged mid-dorsals (46), weak collar (45.2) and pointed, keeled ventrals (49.2). A number of genera have entered habitats with low, dense, coarse and sometimes spiny vegetation and have developed rather stream-lined body forms and modifications that improve protection from mechanical damage (Arnold, 1973), such as collar reduction (45.2, 45.3) and large dorsal and lateral scales (46, 47) that are keeled, lanceolate and strongly overlapping. Among these are *Psammodromus*, *Adolfus alleni*, and members of *Tropidosaura*, *Ichnotropis* and *Ophisops-Cabrita*. Three different stocks, *Meroles-Aporosaura*, *Acanthodactylus* and *Eremias*, have invaded soft sand habitats and produced many parallels in such features as lateral scale rows on the fingers and toes that form supporting fringes (53.1–53.2, 54.1–54.2). Finally, large size has arisen independently in *Gallotia*, *Lacerta jayakari*, *Lacerta lepida* and its close relatives, and in the *Lacerta agilis* group. These parallelisms in niche are responsible for a proportion of the many homoplasies in the lacertid data set. In contrast, where lacertids have entered a distinctive niche or larger area of niche space only once, a number of unique states often arises, for instance in the gliding forest lacertid *Holaspis* and in the clade made up of *'Lacerta' echinata*, *Bedriagaia* and *Gastropholis* which occurs in specialised forest niches (Arnold, 1989).

Niche differentiation and the varying quality of morphological phylogenies in different groups

In some sections of the Lacertidae, ecological differentiation is rather subtle, for instance in *Podarcis* and many members of *Lacerta* in southern Europe and neighbouring areas (Arnold, 1987). Species differ in fairly modest aspects of spatial niche and in relatively small-scale climatic parameters, and there is evidence of considerable ecological parallelism. As might be expected from this, morphological variations tend to fairly restricted and homoplasious, and reconstruction of phylogeny is often difficult. In contrast, assemblages like *Meroles-Aporosaura* which show clear and striking niche differentiation are morphologically diverse without much homoplasy and relationships are much easier to discern.

Resemblances between advanced lacertids and macroteiids

A number of characters that occur in advanced lacertids are common in macroteiid lizards, or are paralleled by analogous states. They are absent from most primitive lacertids and the greatest proportion is found in advanced Saharo-Eurasian forms like *Acanthodactylus*. Among these features are a large nasal opening to the skull (1), a complex septomaxilla (2), fused frontal bones (4), relatively simple fronto-parietal suture (7), posterior extension of parietal bone near mid-line not extensive (11), absence of a quadratojugal process (15), large exposure of the anterior part of the jugal bone (16), no marked sexual variation in the number of presacral vertebrae (28, among advanced lacertids present in a few *Acanthodactylus* species only), anterior autotomic vertebrae with two pairs of diverging transverse processes (31.3), more than two rows of scales on digits (53, 54), subdigital lamellae keeled (55), tongue often pale (61), anterior section of kidney expanded (64, see Cope, 1900, for teiids), m. retractor lateralis anterior inserting laterally in front of vent (66), course of ulnar nerve 'varanide' (81.2). As already noted, the lacertids that possess a high proportion of these features are usually found in relatively xeric habitats. This is also true of many macroteiids. So there may possibly be a functional basis for some of these parallelisms.

Skull characters and ontogeny

Many features of the skulls of most advanced lacertids are similar to states often found in juveniles of some more primitive forms. Amongst these are a large nasal opening (1), narrow interorbital area, simple fronto-parietal suture (7), short, broad parietal area (8,9), restricted cranial osteoderms (11) often including the supraocular ossification, and reduced quadratojugal process (15). These apparently paedomorphic features, where development has been retarded, occur alongside others where ontogenetic change extends further than is usual in primitive taxa (acceleration). This is true for instance of frontal fusion (4) and, where it occurs, fusion of the postfrontal and postorbital bones (12). Heterochronic change of this kind, where new adult features develop by phylogenetic changes in the relative timing of developmental events, appears to be a common source of evolutionary change in reptiles.

NOMENCLATURE

Binomial nomenclature attempts to fulfill two often irreconcilable purposes: firstly, to provide species with a unique and stable name, so that they can easily be referred to and information concerning them readily located; secondly, to give some idea of the relationships of species through their generic allocation (ideally, genera should be holophyletic groups). Difficulties inevitably arise when views on relationships and generic assignment change, resulting in alteration in species names. Such changes, of course, produce few problems for taxonomists or specialists in the assemblage concerned, but they are confusing for most other biologists and laymen, who may constitute the majority of users of the names. As things stand, all that can be done to ameliorate the problem is to alter generic allocation only when the evidence for such a change is very strong, and to take likely inconvenience into account before doing so. Obviously, far less trouble is caused when an obscure species rarely mentioned in the literature has its name altered than when the same thing occurs to a very well known one.

Ophisops Ménétriés, 1832 and *Cabrita* Gray, 1938

These nominal genera share a wide range of derived features, including the presence of an extremely large, transparent 'window' in the lower eyelid which, in this extreme form, is found nowhere else within the Lacertidae. There can be no doubt that they constitute a holophyletic group and *Cabrita* is distinguished from *Ophisops* only by its eyelids not being completely fused together as they are in the latter. This is a primitive condition and cannot be used to define a holophypetic group. Moreover, the two species that constitute *Cabrita* are each more closely related to particular species of *Ophisops* than they are to each other. *Cabrita jerdonii* Beddome, 1870 is allied to *Ophisops jerdoni* Blyth, 1853 and *Ophisops beddomii* (Jerdon, 1870), while the relationships of *Cabrita leschenaultii* (Milne-Edwardes, 1829) lie with *Ophisops microlepis* Blanford, 1870. Therefore, *Cabrita* cannot be regarded as a separate genus and is relegated to the synonymy of *Ophisops*. As *Cabrita jerdonii* shares a trivial name with a species already in *Ophisops*, and acquired it later, a new one is necessary. I propose *Ophisops nictans*, the name meaning 'blinking', in reference to the ability of this species to open and close the eyes, unlike most of its congeners.

Meroles Gray, 1838 and *Aporosaura* Boulenger, 1887

As argued elsewhere (Arnold, in press), there is good evidence that *Aporosaura anchietae* is the sister group of a clade made up of three advanced species of *Meroles*, namely *M. ctenodactylus* (A. Smith, 1838), *M. cuneirostris* (Strauch, 1867) and *M. micropholidotus* (Mertens, 1938). Continuing to exclude the monotypic genus *Aporosaura* from *Meroles* would consequently make the latter paraphyletic. Furthermore, many of the distinctive features of *Aporosaura* are clearly foreshadowed in advanced *Meroles*, and for these two reasons I propose to transfer it to this genus. It is regrettable in many ways to alter a binomial which has stood for over a century, but such a change would reflect the clearly established relationships of the species, and may not cause too much inconvenience as usages of the name *Aporosaura anchietae* have been quite restricted. Also, the fact that the species has a distinctive trivial name within the Lacertidae makes confusion less likely.

Equatorial African lacertids

The nomenclature of these forms is discussed elsewhere (Arnold, 1989). Briefly, *Gastropholis*, *Bedriagaia* and *'L.' echinata* form a very well defined clade and are all placed in the first genus. *'L.' jacksoni* is clearly more closely related to other members of the Equatorial African group of lacertids than it is to any Palaearctic *Lacerta*, and consequently needs to be reallocated. While the most plesiomorphic member of the total Equatorial African clade, *'L'. jacksoni* is, on balance, more likely to be related to *Adolfus* than to *Gastropholis* in its new sense and is consequently transferred to the former. *Holaspis guentheri* raises potential difficulties. It is morphologically very distinct and has many autapomorphies, but may well be the sister taxon of *Adolfus africanus* and *A. vaueresellii*. Leaving it is a monophyletic genus could consequently make *Adolfus* paraphyletic. However, if *Holaspis* and *Adolfus* were merged, the law of priority would demand that the four species of *Adolfus* were transferred to *Holaspis*, with consequent name changes, and the great distinctiveness of *Holaspis guentheri* would cease to be emphasised. More worryingly, the case for regarding *Holaspis* as sister taxon of two of the species of *Adolfus* is not entirely conclusive, so there is a risk that further taxonomic changes are possible. For these reasons, I think it is best to retain *Holaspis* as a monotypic genus and leave *Adolfus*, which is rather poorly defined, as probably paraphyletic for the present. Paraphyly could be avoided by splitting *Adolfus*, confining the name to the type species *A. africanus* and to *A. vaueresellii*, and giving separate generic allocations to *alleni* and *jacksoni*. But such a course would create new names, separate generally similar forms and may not be permanent since the relationships of these species are yet to be very strongly substantiated.

Takydromus Daudin, 1802 and *Platyplacopus* Boulenger, 1917

Boulenger (1917) separated *Platyplacopus* from *Takydromus* on the basis of the structure of the digits. Examination of the members of both nominal genera, shows considerable variation in this feature and it is not possible to delineate the two taxa clearly. Furthermore, separation of *Platyplacopus* appears to make *Takydromus* paraphyletic. The species of *Platyplacopus* are consequently returned to *Takydromus*.

Podarcis

For a long time, *Podarcis* was treated as a subgenus of *Lacerta* (e.g. Boulenger, 1916) but was subsequently raised to full generic status (Arnold, 1973). As understood here, it is made up of fifteen species which share a number of derived features and, although none of these are unique, there is little doubt that the group is holophyletic. Moreover, its members are very alike morphologically, have a close biochemical resemblance (p. 235) and are also relatively similar in many aspects of their ecology and biogeography. This general uniformity means that they are often referred to collectively and it is therefore convenient to have a distinct name for them and to reflect their relationship in their binomials, especially as the separation of *Podarcis* is now generally accepted.

Böhme (1984, 1986) has reviewed in some detail the merits of removing *Podarcis* from *Lacerta*. While continuing to recognise it as separate, he notes that some of its distinctive features also occur among members of the genus *Lacerta*, which are superficially similar, and also in *Psammodromus* and *Gallotia*. There are eleven probably derived features of *Podarcis*, as defined above: jugal bone stepped (17), sternal fontanelle heart-shaped (26.2), anterior autotomic caudal vertebrae C-type (31.3), postnasal scale single (32), parietal scale extending to anterior edge of parietal table (39.2), first supratemporal scale often narrow (st), strong sexual dichromatism (sd), hemipenis with long lobes (72), hemipenis with large lips (73), hemipenial micro-ornamentation of recurved spines (78.2), oviducts entering genital sinus at its tips (80). Among other primitive western Palaearctic lacertids that have more than one or two of them, the features are distributed in the following way (ones that are not universal or present in a rather different form in *Podarcis* are placed in parentheses). *Lacerta andreanszkyi—32, 39.2, 73, 78.2,* st; *L, perspicillata*—39.2, 73, 78.2, st; *L. dugesii*—39.2, (78.2), st, (sd); *L. danfordi*—31.3, 72, 73; *L. vivipara*—32, 39.2, (sd); *Psammodromus*—31.3, 32, 39.2, 72, 73, 78.2, 81.2; *Gallotia* – 31.3, 32, (39.2), 72, 78.2, (st) (sd) Resemblance between *Podarcis* and *Psammodromus* and *Gallotia* is relatively strong, but these groups have distinctive features of their own and their relationships certainly appear to lie elsewhere. In the case of the species of *Lacerta*, none shares more than a small proportion of the distinctive features of *Podarcis*, so there is consequently a good case for recognizing the latter as a separate entity.

As noted (p. 235), Richter (1980) recognised *Lacerta dugesii* and *Lacerta perspicillata* as being closely related and made them the sister group of *Podarcis* as understood above. He regarded the two units as subgenera, *Teira* and *Podarcis* s. str. and included them both in an expanded genus *Podarcis* s. lat., a course that was followed by Böhme (1984, 1986). In fact, as we have seen, *Lacerta dugesii* and *L. perspicillata* possess only a small proportion of the distinctive features of *Podarcis* in its narrow sense and their inclusion consequently dilutes a very uniform group. My inclination would be to exclude them from the genus.

Primitive Palaearctic genera and the problem of *Lacerta*

Most genera within the primitive Palaearctic assemblage are clearly holophyletic and well defined. These include the long-established *Algyroides* and *Psammodromus*, *Takydromus* (as defined above), *Podarcis* and *Gallotia*, which like *Podarcis* was long regarded as a subgenus of *Lacerta* (Boulenger, 1916) but subsequently raised to full generic status (Arnold, 1973). All these taxa are now generally accepted, leaving the other primitive western Palaearctic forms as a single genus, *Lacerta* s. lat. This is undoubtedly paraphyletic, for advanced Ethiopian and Saharo-Eurasian lacertids and all or most of the genera listed at the beginning of this section appear to have arisen from within it. Ideally therefore, in terms of expressing relationship, *Lacerta* s. lat. should be broken up into holophyletic units, attaching species if necessary to taxa which have sprung from it. Regrettably, such a course is not easy. As we have seen, some species could be attached to *Podarcis* by expanding it, and the same could be done in some other instances. But, elsewhere, relationships within *Lacerta* s. lat. are rarely known with any certainty so that the supposed holophyletic groups produced are likely to be of doubtful validity or very small. To give all these generic status would make for instability and split *Lacerta* s. lat. into many fragments. It seems better, for the present, to accept *Lacerta* s. lat. as an admittedly paraphyletic assemblage confined to the Palaearctic region and employ subgenera within it if supposed relationship is to be formally emphasised. A number of suitable names are already in use: *Apathya* Méhely, 1909 (Type species: *Lacerta cappadocica*); *Archaeolacerta* Mertens, 1921 (Type species: *Lacerta bedriagae*); *Lacerta*, Linnaeus, 1758 s. str. (Type species: *Lacerta agilis*); *Omanosaura* Lutz, Bischoff & Mayer, 1986 (Type species: *Lacerta jayakari*); *Teira* Gray, 1845 (Type species: *Lacerta dugesii*); *Thimon* Tschudi, 1836 (Type species: *Lacerta lepida*); *Zootoca* Wagler, 1830 (Type species: *Lacerta vivipara*).

'Lacerta australis' and *'Lacerta' rupicola*

These two South African species have ranges very distant from the rest of *Lacerta* s. lat., especially when the Equatorial African forms once assigned to the genus have been reallocated. Also the South African species share a number of features with other Ethiopian lacertids which are not found in the apparent closest Palaearctic relatives, namely *Lacerta jayakari* etc. They consequently deserve separate generic status and I propose the name *Australolacerta* for them with the type species *Lacerta australis* Hewitt, 1926.

Suggested divisions of the Lacertidae

Two suggestions have recently been made that would divide the Lacertidae. But, as argued previously (Böhme, 1981; Böhme, Hutterer & Bings, 1985) both should be rejected. Shcherbak (1975) proposed that the subfamily Eremiainae should be recognised for the following genera: *Lampreremias* (= *Heliobolus*), *Pseuderemias*, *Taenieremias* (now assigned to *Acanthodactylus*), *Mesalina* (= *Mesalina* and *Pedioplanis*), *Meroles* and *Eremias*. This taxon would be paraphyletic, since *Ophisops* (including *Cabrita*) and most species of *Acanthodactylus* would be excluded. The recognition of the Eremianiae would also make the rest of the Lacertidae paraphyletic and divide the family in an arbitrary manner. Cano, Baez, Lopez-Jurado & Ortega (1984) suggested that *Gallotia* should be placed in a separate family, the Gallotiidae, on the grounds that the genus has a distinctive karyology, but the difference involved is relatively trivial and *Gallotia* is no more distinctive than many other lacertid genera. As with Eremiainae, the recognition of Gallotiidae would make the rest of the Lacertidae paraphyletic.

Acknowledgements. A large number of people have helped me investigate lacertids, either obtaining critical specimens, giving me access to collections in their care, or making loans of material. In other cases information and opinions were freely shared. I am consequently most grateful to the following. A. d'A. Bellairs, A. Gentry, C. J. Humphries and G. Underwood (London), B. C. Groombridge (Cambidge), E. E. Brygoo (Paris), M. S. Hoogmoed (Leiden), G. Peters and R. Günther (Berlin), W. Böhme and W. Bischoff (Bonn), K. Klemmer (Frankfurt), U. Joger (Darmstadt), U. F. Gruber (Munich), J. Eiselt and F. Tiedemann (Vienna), B. Schätti (Geneva), B. Lanza and M. Poggesi (Florence), E. Balletto (Genoa), J. A. Valverde, J. Castroviejo and P. W. Hopkins (Seville), Y. L. Werner (Israel), J. Gasperetti (Jeddah), M. D. Gallagher (Muscat), W. Ross (Ely), A. Disi (Amman), D. Broadley (Bulawayo), W. Haacke (Pretoria), W. R. Branch (Port Elizabeth), R. Auerbach (Gaberone), R. C. Drewes, A. E. Leviton and J. Vindum (San Francisco), R. Estes and R. Etheridge (San Diego), J. Wright and R. Bezy (Los Angeles), R. B. Huey (Seattle), R. F. Inger and H. Marx (Chicago), C. Gans (Ann Arbor), T. M. Uzzell (Philadelphia), C. J. McCoy (Pittsburgh), R. G. Zweifel, G. W. Myers, S. B. McDowell and M. Hecht (New York), E. E. Williams, P. Alberch and J. Rosado (Harvard), G. Zug (Washington) and A. E. Greer (Sydney).

Among my colleagues in the Reptile and Amphibian Section at the British Museum, A. F. Stimson, C. J. McCarthy, B. T. Clarke and J. C. Dring prepared specimens and X-rays and gave advice on various herpetological matters. Nearly all the illustrations were produced by E. O. Z. Wade. I am grateful to R. Estes, C. J. McCarthy, G. Underwood and A. C. Wheeler for reading the manuscript.

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Manuscript accepted for publication 12 September 1988

APPENDIX 1

Evidence for polarity of characters.

The following indicators of polarity are used.

1. Outgroup indicators
   - a. State widespread in tetrapods or at least lizards.
   - b. State universal or nearly so in scincomorphs apart from lacertids.
   - c. State found in majority of scincomorphs apart from lacertids.
   - d. State present in primitive members of scincomorph families, apart from lacertids.
2. Outgroup criterion within studied group.
3. Ontogeny.
4. Overall commonality: present in over 80% of taxa; brackets indicate present in less than 80% but more than 50% of taxa.
5. Universal or common state in primitive Palaearctic forms.
6. Polarity indicated by tree of African and advanced lacertids produced by compatibility analysis.
7. Polarity indicated by tree of Psammodromus and its relatives produced by compatibility analysis.

* indicates characters with good polarity evidence from other sources used to orientate trees produced from compatibility analysis.

		Polarity indicators									
Primitive state of character		1a	1b	1c	1d	2	3	4	5	6	7
1. Nasal opening of skull small	1			+			–	(+)	+	+	
2. Septomaxilla simple	2				+			(+)	+	+	
3. Medial depression on snout absent	3		+					(+)	+	*	
4. Frontal bones unfused	4	+			+		+	(+)	+	*	
5. Dorsal process of maxilla unembraced	5		+					(+)	+	*	
6. Anterior descending frontal processes present	6	+		+		+		+	+		
7. Fronto-parietal suture complex	7			–			–		+	+	
8. Osteodermal area of parietal bone relatively long	8	unsurveyed						(+)	+	+	
9. Osteodermal area of parietal bone relatively narrow	9	unsurveyed						(+)	+	+	
10. Pineal fontanelle present	10	+		+			(+)	+	+	*	
11. Cranial osteoderms to back of parietal bone	11			–			–		+	*	
12. Postorbital and postfrontal bones unfused	12	+					+	(+)	+		
13. Squamosal-parietal contact absent	13			+					+	+	
14. Squamosal bone shallow	14			+					+	+	
15. Quadratojugal process distinct	15							(+)	+	+	
16. Lateral exposure of anterior jugal small	16			+				(+)	+	+	
17. Lower border of jugal unstepped	17		+					+	+		
18. Inner crest of jugal visible behind ectopterygoid	18			+				+	+		*
19. Ossification of temporal scales absent	19			+			+	+	+	+	
20. Lateral teeth with one or two cusps	20			+		+		+	+		
21. Radial portion of scleral ossicle 14 present	21		+					+	+	+	
22. Continuity of clavicle loop varying intraspecifically	22			–			+	(–)	+	+	+
23. Medial expansion of clavicle large	23			+				+	+		
24. Arms of interclavicle not directed backwards	24			+				+	+		

		Polarity indicators									
Primitive state of character		1a	1b	1c	1d	2	3	4	5	6	7
25. Interclavicle unflanged	25			+				+	+		
26. Sternal fontanelle large and elliptical	26			−		+	+	+	+	+	
27. Xiphisternal cartilages close together	27		(+)					(+)	+	*	
28. Sexual variation in number of presacral vertebrae	28	−	−			+		+	+	+	+
29. Few short free dorsal ribs	29								+	+	
30. Inscriptional ribs often present	30			+					+	+	
31. Both A and B pattern caudal processes present	31		−					−	+	+	
32. Postnasal scales two	32			−				+		+	+
33. Postnasal and supranasal separated beneath nostril	33			+				(+)	+	+	
34. Lower postnasal not contacting rostral	34		+					(+)	+	*	
35. Supranasal not contacting loreal	35	both widespread						+	+		
36. Extended lower postnasal not divided	36			(+)		+		+	+		
37. Rostral scale wide	37	unsurveyed				+		+	+	+	
38. Second supraciliary scale not elongate	38	+	+			+		+	+	+	
39. Lateral border of parietal scale within edge of table	39			+		+			+		
40. Occipital normal	40			(+)		+		+	+		
41. Interparietal normal	41			−		+		+	+		
42. No window in lower eyelid	42			+		+		+	+	+	
43. Masseteric scale present	43		−					−?	+		+
44. Five chin shields	44			+				+	+		
45. Collar well developed with granules beneath	45							+	+	+	+
46. Mid-dorsal body scales small	46							+	+	+?	
47. Lateral body scales small	47							+	+	+	
48. Six or eight longitudinal rows of ventral scales	48			+?	+	+		(+)	+	+	

		Polarity indicators									
Primitive state of character		1a	1b	1c	1d	2	3	4	5	6	7
49. No keeling on ventral scales	49		+					+	+	*	
50. Ventral scales in straight longitudinal rows	50		+			+		+	+		
51. Femoral pores unreduced	51			+		+		+	+		
52. Scales bearing femoral pores flattish	52		+					+	+	+	
53. No lateral scale rows on fingers	53			+		+		+	+		
54. No lateral scale rows on toes	54			+		+		+	+		
55. Subdigital lamellae smooth	55			+				+	+	+	
56. Axillary mite pocket absent	56			+				+	+		
57. Post-femoral mite pocket absent	57			+				+	+		
58. Scales bordering ventral mid-line of tail small	58		+					+	+	+	
59. Body scale micro-ornamentation coarsely striate	59			+				+	+		
60. Outer ventrals with blue pigment	60								+		
61. Tongue predominantly dark	61			−					+		+
62. Postnasal area thin in horizontal section	62			+				+	+	+	
63. Nasal vestibule short	63			+				+	+	*	
64. Anterior kidney short	64			+				+	+	+	
65. Posterior kidney extending well beyond vent	65			+				+	+	+	
66. RLA muscle insertion near mid-line	66			−					+		
67. RLA muscle not enlarged in front of vent	67			+				+	+		
68. RLA muscle not attaching to base of hemipenis	68			+				+	+		
69. No thoracic fascia	69			+					+	+	
70. No hemipenial armature	70	+	+						+		
71. Transverse section of hemipenial lobes simple	71	+	+						+		
72. Hemipenial lobes relatively short	72								+		

		Polarity indicators									
Primitive state of character		1a	1b	1c	1d	2	3	4	5	6	7
73. Hemipenial lips moderate or small	73			+					+		
74. Hemipenial connectors not close to clavular tips	74								+		
75. Medial side of hemipenis not reduced	75	+	+			+		+	+		
76. Lateral side of hemipenis not reduced	76	+	+			+		+	+		
77. Hemipenis without large pointed papillae	77			+				+	+		*
78. Hemipenial microornamentation crown-shaped	78										+
79. Female genital sinus bilobed	79			+					+	+	
80. Oviducts exit ventrally	80								+		
81. Ulnar nerve ‘Lacertide’	81	+		+					+	*	
82. Lateral septum on bodenaponeurosis	82		+					+	+		*
83. Usually mute	83			+				+	+		*
84. Flank of female bitten in copulation	84					+		+	+	+	+

APPENDIX 2

Distribution of characters used in analysis (see p. 216)

0 – Primitive state
1 – Derived state
V – character variable
— – no data.

Appendix 2 (part a)

	Character Nos.																	
	1	2.1	2.2	2.3	2.4	3.1	3.2	4	5	6.1	6.2	7	8	9	10.1	10.2	11	12
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophisops-Cabrita	1	1	1	1	1	1	1	1	1	V	V	1	1	1	0	0	1	0
Mesalina	1	1	1	1	1	1	1	1	1	V	0	1	1	1	0	0	1	0
Acanthodactylus	1	1	1	0	0	1	1	1	1	V	0	1	1	1	0	0	1	V
Eremias	1	1	1	0	0	1	1	1	1	V	0	1	1	1	0	0	V	1
Pedioplanis	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1	V
Meroles-Aporosaura	1	1	1	0	0	V	1	1	1	0	0	1	1	1	0	0	1	1
Pseudieremias	1	1	1	0	0	1	1	1	1	0	0	1	1	1	0	0	1	0
Heliobolus	1	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	1	0
Ichnotropis	1	1	0	0	0	1	1	1	1	1	1	1	1	V	0	0	1	1
Latastia	1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	0	1	0
Philochortus	1	1	0	0	0	0	0	1	1	0	0	1	0	0	1	0	1	1
Nucras	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0
Poromera	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0
Tropidosaura	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0
Holaspis	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0
'*Lacerta*' *australis* etc	0	–	–	–	–	0	0	0	–	0	0	0	0	0	0	0	0	0
Gastropholis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Bedriagaia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
'*Lacerta*' *echinata*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Adolfus alleni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Adolfus africanus etc	0	0	0	0	0	0	0	0	0	V	0	0	0	0	1	1	0	1
'*Lacerta*' *jacksoni*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Takydromus etc	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
Gallotia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Psammodromus algirus	0	1	0	0	0	1	0	0	0	V	0	0	0	0	0	0	0	1
Psamm. hispanicus etc	0	1	0	0	0	1	V	0	0	V	0	0	0	0	0	0	0	1
Lacerta parva etc	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta brandtii	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Podarcis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta andreanszkii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta perspicillata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta dugesii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta danfordi etc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta laevis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta, archaeolacertas	V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta oxycephala	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta graeca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Algyroides	V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta cappadocica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta agilis etc	0	0	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	V
Lacerta princeps	0	0	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	1
Lacerta lepida etc	0	0	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	V
Lacerta jayakari etc	V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta vivipara	0	0	0	0	0	0	0	0	0	V	0	0	0	0	0	0	0	1
Hypo. Ethiopian ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2 (part b)

	13	14	15	16	17	18	19	20	21	22.1	22.2	23	24	25	26.1	26.2	26.3	27
Ancestor	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophisops-Cabrita	0	0	V	1	0	0	0	0	0	0	1	0	0	V	1	1	0	1
Mesalina	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1
Acanthodactylus	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1
Eremias	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1
Pedioplanis	1	1	1	V	0	0	0	0	0	0	1	0	0	0	1	1	0	1
Meroles-Aporosaura	1	1	0	1	0	0	0	0	1	0	1	0	0	0	V	V	V	1
Pseudieremias	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Heliobolus	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Ichnotropis	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Latastia	1	1	0	V	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Philochortus	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Nucras	1	0	0	0	0	0	0	0	0	0	1	V	0	0	0	0	0	0
Poromera	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0
Tropidosaura	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Holaspis	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0
'*Lacerta*' *australis* etc	0	0	0	0	0	0	0	0	–	0	1	0	0	0	0	0	0	0
Gastropholis	V	V	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Bedriagaia	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
'*Lacerta*' *echinata*	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Adolfus alleni	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
Adolfus africanus etc	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
'*Lacerta*' *jacksoni*	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Takydromus etc	V	V	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Gallotia	0	0	0	0	0	0	V	V	0	0	1	0	0	0	0	0	0	0
Psammodromus algirus	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0
Psamm. hispanicus etc	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Lacerta parva etc	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Lacerta brandtii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Podarcis	0	0	0	0	1	0	V	0	0	V	0	0	0	0	1	1	0	0
Lacerta andreanszkii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Lacerta perspicillata	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Lacerta dugesii	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Lacerta danfordi etc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Lacerta laevis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Lacerta, archaeolacertas	0	0	0	0	0	0	0	0	0	V	0	0	0	0	0	0	0	0
Lacerta oxycephala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta graeca	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Algyroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	V	0	0	0
Lacerta cappadocica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta agilis etc	0	0	0	0	1	0	V	0	0	0	0	0	0	0	0	0	0	0
Lacerta princeps	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lacerta lepida etc	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lacerta jayakari etc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta vivipara	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypo. Ethiopian ancestor	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Appendix 2 (part c)

	28	29	30	31.1	31.2	31.3	32	33	34	35	36	37	38	39.1	39.2	40.1	40.2	41.1
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophisops-Cabrita	0	1	1	0	1	1	0	1	1	0	V	0	V	0	0	0	0	0
Mesalina	0	0	1	0	1	1	0	1	1	0	0	0	0	1	1	0	V	V
Acanthodactylus	V	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
Eremias	0	1	1	1	0	0	0	1	1	0	0	1	0	1	1	0	1	0
Pedioplanis	0	1	1	1	0	0	0	1	1	0	0	0	0	1	1	0	0	V
Meroles-Aporosaura	0	1	1	1	0	0	0	1	1	0	0	V	0	V	V	0	V	0
Pseudieremias	0	1	1	1	0	0	0	1	1	0	1	0	0	V	V	0	V	0
Heliobolus	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	V	0
Ichnotropis	0	1	1	1	0	0	0	1	1	0	0	0	V	0	0	0	V	0
Latastia	0	1	1	1	0	0	0	V	0	0	–	0	0	0	0	0	0	0
Philochortus	0	1	1	1	0	0	0	0	0	0	–	0	0	0	0	0	0	0
Nucras	0	V	V	1	0	0	0	1	0	0	–	0	0	0	0	0	0	0
Poromera	0	V	1	1	0	0	0	0	0	0	–	0	0	0	0	0	0	0
Tropidosaura	0	0	1	1	0	0	V	V	0	0	–	0	V	0	0	0	0	0
Holaspis	0	0	1	1	0	0	1	1	0	0	–	0	0	1	1	0	0	0
'*Lacerta*' *australis* etc	0	V	1	1	0	0	0	V	0	0	–	0	0	V	0	0	0	0
Gastropholis	0	0	0	1	0	0	1	1	0	0	–	0	0	1	1	0	0	0
Bedriagaia	0	0	0	1	0	0	1	0	0	0	–	0	0	1	1	0	0	0
'*Lacerta*' *echinata*	0	0	0	1	0	0	1	0	0	0	–	0	0	1	1	0	0	0
Adolfus alleni	0	0	0	1	0	0	1	0	0	0	–	0	0	1	1	0	0	0
Adolfus africanus etc	0	0	V	1	0	0	1	V	0	0	–	0	0	1	1	0	0	0
'*Lacerta*' *jacksoni*	0	0	1	1	0	0	1	0	0	0	–	0	0	1	1	0	0	0
Takydromus etc	0	0	V	1	0	0	V	0	0	V	–	0	V	V	0	0	0	0
Gallotia	1	V	V	0	1	1	1	0	0	0	–	0	0	1	V	0	0	0
Psammodromus algirus	0	0	0	0	1	1	1	0	0	0	–	0	1	1	1	0	0	0
Psamm. hispanicus etc	0	0	0	0	1	1	1	1	0	0	–	0	1	1	1	0	0	0
Lacerta parva etc	0	0	1	0	1	0	V	1	0	0	–	0	0	1	0	0	0	0
Lacerta brandtii	0	V	1	0	1	0	0	1	0	0	–	0	0	0	0	0	0	0
Podarcis	0	0	V	0	1	1	1	0	0	0	–	0	0	1	1	0	0	0
Lacerta andreanszkii	0	0	0	0	0	0	1	0	0	1	–	0	0	1	1	0	0	0
Lacerta perspicillata	0	0	1	0	0	0	0	1	0	0	–	0	0	1	1	0	0	0
Lacerta dugesii	0	V	1	0	0	0	0	0	0	0	–	0	0	1	1	0	0	0
Lacerta danfordi etc	0	1	1	0	1	V	0	0	0	0	–	0	0	1	0	0	0	0
Lacerta laevis	0	0	1	0	0	0	0	0	0	0	–	0	0	1	0	V	0	0
Lacerta, archaeolacertas	0	0	V	V	0	0	V	0	0	V	–	0	0	1	V	0	0	0
Lacerta oxycephala	0	0	1	0	0	0	0	0	0	0	–	0	0	1	0	0	0	0
Lacerta graeca	0	0	1	0	0	0	0	0	0	0	–	0	0	1	0	0	0	0
Algyroides	0	0	1	0	0	0	V	0	0	0	–	0	0	1	V	0	0	0
Lacerta cappadocica	0	V	1	1	0	0	0	0	0	0	–	0	0	0	0	0	0	0
Lacerta agilis etc	0	V	0	0	0	0	V	0	0	0	–	0	0	0	0	V	0	0
Lacerta princeps	0	V	0	0	0	0	0	0	0	0	–	0	0	0	0	V	0	0
Lacerta lepida etc	0	V	0	0	0	0	0	0	0	0	–	0	0	0	0	V	0	0
Lacerta jayakari etc	0	1	1	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0
Lacerta vivipara	0	0	V	1	0	0	1	0	0	1	–	0	0	1	1	0	0	0
Hypo. Ethiopian ancestor	0	0	0	1	0	0	0	0	0	0	–	0	0	0	0	0	0	0

Appendix 2 (part d)

	41.2	42	43	44	45.1	45.2	45.3	46	47	48.1	48.2	49.1	49.2	50	51.1	51.2	52	53.1
Ancestor	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophisops-Cabrita	0	1	1	0	1	1	1	V	V	V	V	0	0	0	0	0	0	0
Mesalina	0	V	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
Acanthodactylus	0	0	1	0	V	0	0	V	V	1	1	0	0	V	0	0	0	1
Eremias	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	V
Pedioplanis	0	V	1	1	0	0	0	0	0	1	1	0	0	V	0	0	0	0
Meroles-Aporosaura	0	0	1	0	V	V	V	0	0	1	1	0	0	V	0	0	0	1
Pseudieremias	0	0	1	1	0	0	0	0	0	V	V	0	0	0	0	0	0	V
Heliobolus	0	0	1	1	V	0	0	0	0	V	0	0	0	0	0	0	0	0
Ichnotropis	0	0	1	0	1	1	1	1	1	1	V	0	0	0	0	0	0	0
Latastia	0	0	1	1	0	0	0	0	0	V	0	0	0	0	V	0	0	0
Philochortus	V	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Nucras	0	0	1	1	0	0	0	0	0	V	0	0	0	0	0	0	0	0
Poromera	0	0	1	1	1	1	0	1	0	1	V	1	1	0	1	0	0	0
Tropidosaura	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Holaspis	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
'*Lacerta*' *australis* etc	0	V	1	0	0	0	0	0	0	V	0	0	0	0	0	0	0	0
Gastropholis	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0
Bedriagaia	0	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0
'*Lacerta*' *echinata*	V	0	1	0	0	0	0	0	0	0	0	V	0	0	0	0	1	0
Adolfus alleni	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0
Adolfus africanus etc	0	0	1	0	0	0	0	1	V	0	0	V	0	0	V	0	0	0
'*Lacerta*' *jacksoni*	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Takydromus etc	0	0	1	V	V	V	0	V	0	V	V	1	V	0	1	1	0	0
Gallotia	0	0	V	0	0	0	0	0	0	1	1	0	0	V	0	0	0	0
Psammodromus algirus	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Psamm. hispanicus etc	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0
Lacerta parva etc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lacerta brandtii	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Podarcis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta andreanszkii	0	0	V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta perspicillata	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Lacerta dugesii	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta danfordi etc	0	0	0	0	0	0	0	0	0	V	0	0	0	0	0	0	0	0
Lacerta laevis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta, archaeolacertas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta oxycephala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta graeca	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Algyroides	0	0	0	0	0	0	0	1	V	0	0	0	0	0	0	0	0	0
Lacerta cappadocica	0	1	1	0	0	0	0	0	0	V	0	0	0	0	0	0	0	0
Lacerta agilis etc	0	0	0	V	0	0	0	0	0	V	0	0	0	0	V	0	0	0
Lacerta princeps	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Lacerta lepida etc	0	0	0	0	0	0	0	0	0	1	V	0	0	0	0	0	0	0
Lacerta jayakari etc	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lacerta vivipara	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypo. Ethiopian ancestor	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2 (part e)

	53.2	54.1	54.2	55	56	57	58	59	60	61	62.1	62.2	63.1	63.2	63.3	63.4	64	65
Ancestor	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ophisops-Cabrita	0	0	0	1	0	V	0	0	1	V	1	1	1	1	1	1	1	0
Mesalina	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Acanthodactylus	V	1	0	1	0	V	0	0	1	1	1	1	1	1	1	1	1	0
Eremias	V	V	V	1	0	0	0	0	1	1	1	1	1	1	1	1	1	0
Pedioplanis	0	0	0	1	V	0	0	0	1	1	1	1	1	1	1	1	1	1
Meroles-Aporosaura	V	1	V	V	0	0	0	0	1	0	1	1	1	1	1	1	V	0
Pseudieremias	0	V	0	1	0	0	0	0	1	1	1	0	1	1	1	0	1	0
Heliobolus	0	0	0	1	0	1	0	0	1	1	1	0	1	1	0	0	1	1
Ichnotropis	0	V	0	1	V	0	0	0	1	0	1	0	1	1	0	0	1	1
Latastia	0	0	0	1	0	V	0	0	1	1	0	0	1	1	0	0	1	1
Philochortus	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0
Nucras	0	0	0	0	0	V	0	0	1	1	0	0	0	0	0	0	1	1
Poromera	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Tropidosaura	0	0	0	0	V	0	0	0	1	0	0	0	0	0	0	0	0	0
Holaspis	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
'*Lacerta*' *australis* etc	0	0	0	0	V	0	0	0	1	0	0	0	–	–	–	–	0	0
Gastropholis	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Bedriagaia	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
'*Lacerta*' *echinata*	0	0	0	0	0	V	0	1	1	1	0	0	0	0	0	0	0	0
Adolfus alleni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adolfus africanus etc	0	0	0	0	0	V	0	0	1	0	0	0	0	0	0	0	0	0
'*Lacerta*' *jacksoni*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Takydromus etc	0	0	0	0	0	0	0	1	1	V	0	0	0	0	0	0	0	0
Gallotia	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0
Psammodromus algirus	0	0	0	0	0	0	0	1	1	V	0	0	1	1	1	1	0	0
Psamm. hispanicus etc	0	0	0	V	0	0	0	0	1	V	0	0	1	1	1	1	0	0
Lacerta parva etc	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Lacerta brandtii	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Podarcis	0	0	0	0	0	0	0	0	0	0	0	0	V	0	0	0	0	0
Lacerta andreanszkii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Lacerta perspicillata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta dugesii	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lacerta danfordi etc	0	0	0	0	0	0	0	0	0	V	0	0	0	0	0	0	0	0
Lacerta laevis	0	0	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta, archaeolacertas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta oxycephala	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lacerta graeca	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Algyroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacerta cappadocica	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Lacerta agilis etc	0	0	0	0	0	0	0	0	1	0	0	0	V	0	0	0	0	0
Lacerta princeps	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Lacerta lepida etc	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Lacerta jayakari etc	0	0	0	V	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Lacerta vivipara	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hypo. Ethiopian ancestor	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

Appendix 2 (part f)

	66	67	68	69.1	69.2	70	71	72	73	74	75	76	77	78.1	78.2	79	80	81.1
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophisops-Cabrita	V	0	1	1	1	1	1	–	–	0	0	0	0	0	0	0	1	1
Mesalina	0	1	1	1	1	1	1	–	–	0	0	V	0	0	0	0	1	1
Acanthodactylus	1	0	0	1	1	1	V	–	–	0	V	0	0	0	V	1	1	1
Eremias	1	0	0	1	0	1	1	–	–	V	0	V	0	0	V	V	V	1
Pedioplanis	1	0	0	0	0	V	V	–	–	0	0	0	0	0	1	V	1	1
Meroles-Aporosaura	1	0	0	V	0	V	V	–	–	0	0	V	0	0	1	V	1	1
Pseudieremias	1	0	0	1	0	1	1	–	–	0	0	0	0	0	1	1	1	1
Heliobolus	1	0	0	1	0	1	1	–	–	0	0	V	0	0	1	1	1	1
Ichnotropis	1	0	0	1	1	1	1	–	–	0	0	0	0	0	1	1	1	1
Latastia	1	0	0	1	0	1	1	–	–	0	0	V	0	0	0	1	1	1
Philochortus	1	0	0	1	V	1	1	–	–	0	1	0	0	0	1	1	1	1
Nucras	V	0	0	1	V	1	1	–	–	0	0	0	0	0	1	1	1	1
Poromera	1	0	0	1	1	1	0	–	–	0	0	0	0	0	1	1	1	1
Tropidosaura	1	0	0	1	V	1	1	–	–	V	0	0	0	0	1	–	–	1
Holaspis	1	0	0	0	0	1	1	–	–	1	0	0	0	0	1	1	1	1
'*Lacerta*' *australis* etc	–	–	–	0	0	1	1	–	–	1	0	0	0	–	–	1	V	1
Gastropholis	1	0	0	1	1	1	1	–	–	0	0	0	0	0	1	1	1	1
Bedriagaia	1	0	1	1	1	1	1	–	–	0	1	0	0	0	1	1	1	1
'*Lacerta*' *echinata*	1	0	1	1	0	1	1	–	–	0	1	0	0	0	1	1	1	1
Adolfus alleni	1	0	0	0	0	1	1	–	–	0	0	0	0	0	1	1	1	1
Adolfus africanus etc	1	0	0	0	0	1	1	–	–	0	0	0	0	0	1	V	1	1
'*Lacerta*' *jacksoni*	1	0	0	0	0	1	1	–	–	0	0	0	0	0	1	1	1	1
Takydromus etc	0	1	0	V	0	0	0	1	0	–	0	0	0	0	1	0	0	0
Gallotia	0	0	0	V	0	0	0	1	0	–	0	0	1	0	1	0	0	0
Psammodromus algirus	0	0	0	0	0	0	0	1	1	–	0	0	0	0	1	0	1	0
Psamm. hispanicus etc	0	0	0	0	0	0	0	0	0	–	0	0	1	1	0	0	0	0
Lacerta parva etc	0	0	0	0	0	0	0	0	0	–	0	0	0	1	0	1	0	0
Lacerta brandtii	1	0	0	0	0	0	0	0	0	–	0	0	0	–	–	0	0	0
Podarcis	0	0	0	0	0	0	0	1	1	–	0	0	0	0	1	0	1	0
Lacerta andreanszkii	1	0	0	1	0	0	0	0	1	–	0	0	0	0	1	0	0	0
Lacerta perspicillata	0	0	0	0	0	0	0	0	1	–	0	0	0	0	1	0	0	0
Lacerta dugesii	1	0	0	0	0	0	0	0	0	–	0	0	0	0	1	0	0	0
Lacerta danfordi etc	0	1	0	0	0	0	0	1	1	–	0	0	0	0	0	0	0	0
Lacerta laevis	1	0	0	0	0	0	0	0	1	–	0	0	0	0	0	0	0	0
Lacerta, archaeolacertas	V	0	V	0	0	0	0	0	0	–	0	0	0	0	V	0	0	0
Lacerta oxycephala	0	0	1	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0
Lacerta graeca	0	0	1	0	0	0	0	0	0	–	0	0	0	0	1	0	0	0
Algyroides	0	0	0	0	0	0	0	0	0	–	0	0	0	0	V	0	0	0
Lacerta cappadocica	0	1	1	0	0	0	1	0	0	–	0	0	0	0	1	0	0	0
Lacerta agilis etc	1	0	0	0	0	0	0	0	0	–	0	0	0	0	V	0	0	0
Lacerta princeps	1	0	0	0	0	0	0	0	0	–	0	0	0	0	1	0	0	0
Lacerta lepida etc	1	0	0	1	0	0	0	0	0	–	0	0	0	0	1	0	0	0
Lacerta jayakari etc	1	0	1	0	0	1	1	–	–	0	0	0	0	0	V	0	0	1
Lacerta vivipara	0	1	0	0	0	1	1	–	–	0	0	0	0	0	0	0	0	0
Hypo. Ethiopian ancestor	1	0	0	0	0	1	1	–	–	0	0	0	0	0	0	1	1	1

Appendix 2 (part g)

	81.2	82	83	84
Ancestor	0	0	0	0
Ophisops-Cabrita	1	0	0	0
Mesalina	1	0	0	V
Acanthodactylus	1	0	0	0
Eremias	1	0	0	0
Pedioplanis	1	0	0	0
Meroles-Aporosaura	1	0	0	V
Pseudieremias	1	0	0	0
Heliobolus	1	0	0	0
Ichnotropis	1	0	V	0
Latastia	1	0	0	0
Philochortus	1	0	0	0
Nucras	1	0	0	0
Poromera	1	0	0	0
Tropidosaura	1	0	0	0
Holaspis	1	0	0	0
'*Lacerta*' *australis* etc	1	–	0	–
Gastropholis	1	0	0	0
Bedriagaia	1	0	0	0
'*Lacerta*' *echinata*	0	0	0	0
Adolfus alleni	0	0	0	0
Adolfus africanus etc	V	0	0	0
'*Lacerta*' *jacksoni*	0	0	0	0
Takydromus etc	0	0	0	0
Gallotia	0	1	1	1
Psammodromus algirus	0	1	1	1
Psamm. hispanicus etc	0	0	1	1
Lacerta parva etc	0	0	0	0
Lacerta brandtii	0	0	0	0
Podarcis	0	0	0	0
Lacerta andreanszkii	0	0	0	0
Lacerta perspicillata	0	0	0	0
Lacerta dugesii	0	0	0	0
Lacerta danfordi etc	0	0	0	0
Lacerta laevis	0	0	0	0
Lacerta, archaeolacertas	0	0	0	0
Lacerta oxycephala	0	0	0	0
Lacerta graeca	0	0	0	0
Algyroides	0	0	0	0
Lacerta cappadocica	0	0	0	0
Lacerta agilis etc	0	1	0	0
Lacerta princeps	0	1	0	0
Lacerta lepida etc	0	1	0	0
Lacerta jayakari etc	1	0	0	1
Lacerta vivipara	0	0	0	0
Hypo. Ethiopian ancestor	0	0	0	0

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Bulletin British Museum (Natural History)
ZOOLOGY SERIES
Vol. 55, No. 2, October 1989

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Bulletin British Museum (Natural History)

Zoology Series

VOLUME 56 NUMBER 1 31 MAY 1990

The *Bulletin of the British Museum of Natural History*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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Fax: 01-938-8709

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

© British Museum (Natural History), 1990

ISBN 0 565 05047 8
ISSN 0007 – 1498

Zoology Series
Vol 56 No 1 pp 1 – 91

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 31 May 1990

Typeset by J & L Composition, Filey, North Yorkshire
Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

Bull. Br. Mus. nat. Hist (Zool) **56**(1): 1–56 Issued 31 May 1990

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Osteology of the Soay sheep

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This project describes the elements of the skeleton of a single breed of sheep, the Soay, using a large sample of more than 60 skeletons and more than 1000 randomly collected bones derived from a single population. It has involved field observation and field collection on the island of Hirta, St. Kilda, Scotland; the maintenance of a small flock at Cambridge, and skeletal preparation, measurement, qualitative assessment and curation in the British Museum (Natural History). In addition, for comparison, a number of goat skeletons were collected from Holy Island, Arran, Scotland. Despite the use of the Soay as a model of primitive domestic sheep for comparison with modern breeds, and with the remains of prehistoric sheep from archaeological sites, no metrical or morphological analysis of the

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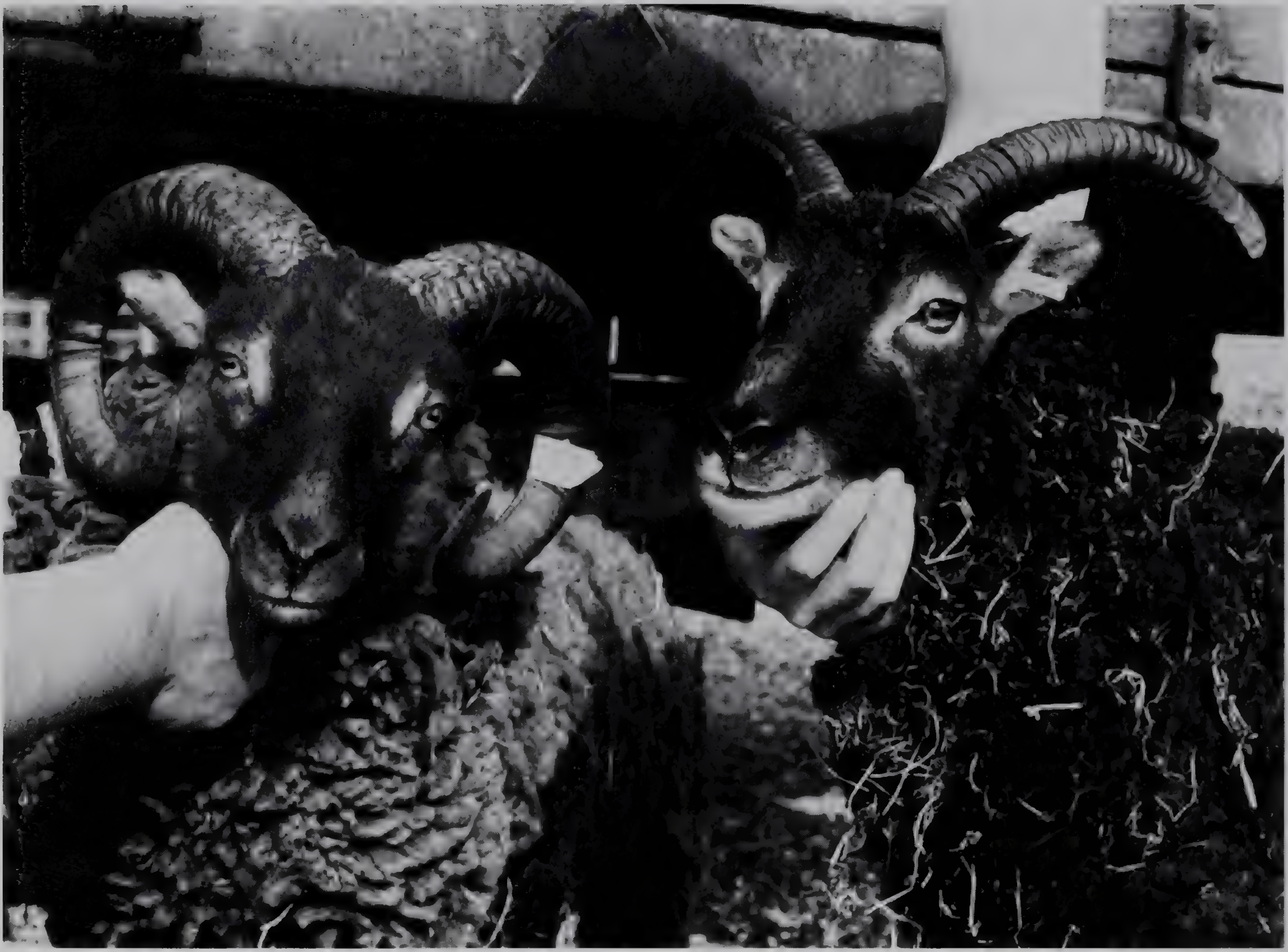


Two Soay sheep photographed at Laundry Farm, Cambridge, in December 1982. Both are three and a half years old. Left: entire ram, light, wild-type colour of fleece; right: male castrate, dark, wild-type fleece.

Soay skeleton has previously been undertaken. Here comparisons and deductions are presented concerning the status of the Soay as a model. A further important part of the project relates to the interpretation of bone collections recovered from archaeological sites where to distinguish sheep from goats aids the reconstruction of palaeoeconomy and palaeoecology. We have examined the anatomical criteria by which the bones of the Soay can be distinguished from those of goats, using the characters that were first observed by Gromova and by Boessneck and his colleagues. The question is whether primitive breeds, that are likely to be similar to the sheep represented on archaeological sites, exhibit the appropriate anatomical features. Rather few totally reliable features could be verified but sets of features are diagnostic. Criteria for distinguishing sex from certain bones were substantiated. The effects of castration of the male on bone and horn development are described and the genetics of hornedness are discussed. The bones have been incorporated into the national collection, and the data base is held as an archive at the British Museum (Natural History).

INTRODUCTION

Historical background

The Soay sheep occupies a special position in the mammalian fauna of Europe. It is derived from domesticated stock but retains many features of wild sheep and until the end of the nineteenth century it survived only as a feral population, of about 200 animals, on the tiny island of Soay in the St Kilda archipelago of the Outer Hebrides, Scotland. The main island of St Kilda is Hirta and this was inhabited until August 1930 when the islanders were evacuated together with their stock. This left the island of Hirta free of livestock until 1932 when the landowner, the Marquess of Bute, transferred 107 Soay sheep of mixed age and sex from the island of Soay to the newly deserted main island. Soay sheep have lived wild on Hirta since that time and for the last 30 years detailed studies have been carried out on their ecology and reproductive behaviour (Jewell, Milner & Boyd, 1974; Jewell, 1986).

The origins of the Soay sheep are unknown but its small slender bones and the structure of the fleece, which closely resembles some finds of prehistoric cloth, suggest that it may be a relic of the sheep that were widespread through Europe in the Bronze Age, around 3500 years before present (Ryder, 1983, p. 47). It is not known when sheep were first taken to the island of Soay; it could have been in the prehistoric period, or in early Christian times when there was much movement in the region, or they could have been taken there by the Vikings. The word 'Soay' or 'Soa' means 'island of sheep' in old Norse, so perhaps there were already sheep on the island when the Norsemen first arrived there.

The sheep on Soay had no contact with humans except when the islanders landed about once a year to catch sea birds. A few sheep were occasionally removed and a number were brought to England at the beginning of this century. They were described by the well known naturalist, H. J. Elwes, in 1913, and he sent some to the Duke of Bedford at Woburn Abbey (Elwes, 1913). From that time the Soay sheep became well known as park animals and today there are about 4000 Soays on farms and parks throughout Britain.

Although classified as a domestic sheep, *Ovis aries* L., the Soay has great zoological interest in representing an early stage in the evolution of modern commercial sheep from the wild ancestor, *Ovis orientalis* Gmelin, 1774 (Clutton-Brock, 1987).

The distinctive features of the Soay sheep, its short tail, brown colouring, annually moulting coat and, typically, large black horns in the male, are characters shared with wild sheep. It is known, however, that wild sheep were not present in Europe in post-glacial times and that they were brought there as domesticated animals from western Asia in the late Mesolithic and early Neolithic. These sheep probably differed little from the wild species but with poor feeding and the stress of captivity they soon became much reduced in size so that their bones, recovered from archaeological sites, closely resemble those of the present day Soay. As long ago as 1931, D. M. S. Watson likened the abundant sheep remains from the late Neolithic site of Skara Brae on Orkney to the bones of the Soay (Childe, 1931).

The Soay is very similar in body proportions, coloration, and fleece to the mouflon *Ovis musimon* Pallas, 1811, of Corsica and Sardinia except that it is a rather smaller animal. The average weight of the Soay for males in good condition is 36 kg and 25 kg for females, while a mouflon has a maximum weight of about 55 kg (Jewell *et al.*, 1974, p. 88). The Soay has two colour phases, a dark form which is closely similar to the colour of the mouflon, and a light form which is beige-brown in colour. There are also two types of fleece which correspond to those described for textiles as 'hairy medium' and 'generalized medium' (Ryder, 1983, p. 47); that is they can be hairy or woolly. The fleece is self-shedding in the early summer as in wild sheep, in the mouflon and in some other primitive breeds.

The Corsican and Sardinian mouflon used to be considered as a relic of an endemic wild species, but it is now realized that, as there are no authentic Pleistocene fossils of sheep from the Mediterranean region, the mouflon, like the Soay, must be an anciently feral sheep that was introduced in the prehistoric period (Poplin, 1979). It has survived in its very primitive form on Corsica and Sardinia because it has never interbred with improved stock. Ryder (1983, p. 48) considers that the mouflon has a fleece that is very little altered from that of the wild sheep.

The Soay sheep is the smallest and one of the last relict populations of primitive domestic sheep that survived from the prehistoric period until the last century in the western and northern isles of Britain, in Iceland, and in Scandinavia, as well as in the highlands of Scotland. Ryder (1983) regards some of these sheep, for example the Orkney sheep from North Ronaldsay, as survivals of a late Iron Age type because their fleece is rather more developed than it is in the Soay. However, sheep similar to the Soay did survive on the smallest of the Faroe islands, known as Little Dimun, until the year 1865 (Hatting, 1983). Historical references to these sheep are cited in Jewell (1980).

The study of the feral Soay sheep on the island of Hirta was begun in 1959 and still continues. Since then a sample of the lambs born every spring has been given coloured and numbered ear tags. Carcasses of animals of known age are therefore frequently encountered during field work. The sheep often die in the shelter of dry stone chambers known as cleits, and then become mummified, so preserving the skeleton intact.

Events in the life cycle of the Soay on Hirta follow a strict annual cycle. The great majority of adult deaths occur in March, after the rigours of winter when grazing is at a minimum. Almost all lambs are born within a fortnight in April, so that births and deaths are close together in time and the sheep live for a given number of whole years (Jewell *et al.*, 1974, p. 364). As J. Morton Boyd has written (in Jewell *et al.*, 1974), 'in winter and spring both people and sheep on St Kilda were in a state of distress through malnutrition. This inexorable cycle of winter poverty and summer recovery to which the Soay sheep today are subject was at the heart of the problem of human survival at St Kilda since it first became settled by humans'.

The osteological study

The collection of Soay sheep bones from Hirta provides a large number of skeletal elements from a single, reproductively isolated population in which variation is individual and sexual but is unaffected by artificial selection and breed differences. The material is therefore ideal for the categorization of osteological features specific to sheep, which can be used to distinguish the remains of sheep from those of goats in assemblages retrieved from archaeological sites. Hence it was appropriate for a large part of this osteological study to be devoted to the definition of sheep-specific characters in the Soay material.

Bones of the Soay sheep have been used for nearly a hundred years, since first measured by Pitt Rivers (1898), for the identification, ageing, and general description of the remains of sheep from archaeological sites, and yet the skeleton of the Soay itself has never been described osteologically, nor its elements quantified. Recently, however, two projects have been undertaken to establish the parameters of the Soay skeleton, one being the present work on material collected from feral sheep on Hirta and the second project being an analysis by S. Payne and A. J. Legge of skeletal material from mainland 'park' Soays bred at the Agricultural and Food Research Council Institute of Animal Physiology at Babraham, Cambridge. No previous large-scale metrical analyses of the skeletons of a single breed of sheep have been carried out. The nomenclature of the bones throughout the work follows that of Hughes & Dransfield (1953).

MATERIALS AND METHODS

Collection of the material

Soay sheep skeletons and bones

The population of Soay sheep on the island of Hirta goes through cycles of 'boom and bust' producing heavy mortality in certain years. In the winter of 1978/79 there was very heavy mortality and 224 tagged and therefore known-age sheep were counted dead. A selection of these was stored in the cleits and 47 skeletons later shipped back to the British Museum (Natural History) to be added to the collection that already existed.

Over the years, between 1959 and 1978, a collection of over a thousand separate bones, picked up at random, was also made. Long bones of the appendicular skeleton with fused epiphyses, skulls, mandibles, and scapulae predominated in this collection. (It should be noted that in the years 1978, 1979 and 1980, 72 male sheep on Hirta were castrated (Jewell, 1986) but the *random* collection of bones was made before any dead castrates could have contributed to this material. Two one-year old castrate *skeletons* collected in 1979, were, however, added to our study material.)

In a small flock of Soay sheep originally maintained at the Royal Holloway College (London University), 7 male lambs were castrated shortly after birth. The sheep in this flock were derived from an importation of animals direct from Hirta in 1963. They were later moved to the University of Cambridge where they were killed to give a series of known ages up to nine years old (see Table 1), and the skeletons were presented to the British Museum (Natural History). To these was added the skeleton of a castrate aged 6 years 4 months from Babraham, which had been presented to the British Museum (Natural History), to increase the size of the sample. It was considered permissable to include this skeleton in the analysis because its size was within the range of the other castrates and it had been raised under similar grazing conditions.

Soay sheep horns and horn cores

Information and measurements on the horns and horn cores of the Soay sheep were obtained from the following sources:

1. Measurements were recorded in the field, on Hirta, of over 80 known-age sheep that had died in the spring of 1979. Where possible the horn sheaths were pulled off to allow measurement of the horn cores. Only the horn sheaths of these individuals were collected, not the skulls or skeletons.
2. Visual inspection was made of the growth of the horns on 44 living adults with lambs at foot, on Hirta, in 1980.
3. Records of the annual incremental growth in the horns of the 7 castrated Soays kept at Cambridge were made through 1978–81. After these animals had been killed their horn sheaths were pulled off and the horn cores were measured (see Appendix).
4. Measurements were taken in the British Museum (Natural History) of the horn cores from the collection of cleaned skulls (see Appendix).

Goats

The goat material used in the study was collected in 1982 from a feral flock on Holy Island, Arran, Scotland, by Sheila Cameron who very kindly presented 7 skeletons to the Museum.

The metrical analysis

The parts of the skeleton that were used in the project are the horns, horn cores, skull, atlas, axis, scapula, pelvis, and limb bones. The vertebrae (other than the atlas and axis), carpal bones and sesamoid bones were excluded.

Whenever the material was available, ten known-age male skeletons and ten known-age female skeletons were used. The bone elements of only one side of each skeleton were measured. To supplement these and increase the size of the sample 20 examples of each element (of unknown age and sex) were taken without selection from the randomly collected sample, except to be all from left or right side. In the archive the origin of each bone from left or right side is recorded.

The dimensions of every bone were recorded in millimetres (mm) using the standard measurements of Driesch (1976). The majority of the measurements were recorded using an osteometric board and digital calipers; at the beginning of the project these were linked to a flexiwriter that produced both hard copy and punched paper tape for reading by the Museum's Varian computer. During the course of the work this Varian computer was exchanged for a PDP computer which could not transcribe paper tape, so the final measurements, those on the older castrate skeletons, were taken on manual calipers. The precise positions of the measurements are shown on the outline drawings of each element.

Despite the need to calibrate the digital calipers and osteometric board every time they were used, and the fact that a number of different people assisted with the measurements, tests for consistency showed that deviations were insignificant. The summaries of the measurements are given in the Appendix, while the complete data base is held as an archive in the British Museum (Natural History), and is available on request.

Criteria for ageing

One of the most important deductions to be made from any assemblage of animal remains from an archaeological site is the age at which the animals had died or had been killed. From this assessment of age the so-called 'slaughter pattern' or 'harvest profile' of the site can be calculated, this being a valuable indication of the economic basis of the site. In order to estimate the age of a jaw or bone at death it is essential to have appropriate comparative material of known age.

Usually the degree of fusion is assessed on prepared skeletal material but it can also be done by radiography. An early attempt by Smith (1956) to establish the times of fusion of the bones of Clun Sheep by X-rays of living animals produced results that differed considerably from those of earlier reports. Whether this was because of the different methods used or whether it was due to a genuinely wide range in the times of fusion has not been determined.

The standard work is Silver (1969) who assembled tables of ages of tooth eruption and epiphysial fusion in the horse, ass, ox, sheep, pig and dog. These give a broad indication of the ages of teeth and limb bones in these animals but much further detailed work needs to be carried out. In 1978 and 1979 two seminars were held in Oxford on the subject of ageing and sexing of animal bones and teeth (Wilson, Grigson & Payne, 1982) but no new detailed information was made available on sheep, one of the difficulties being the lack of distinguishing features for the distinction of sheep from goat jaws.

Although there has been little or no work carried out, during the last 20 years, on the ages at which the teeth of sheep erupt, Payne has made an exhaustive study of the ageing of goat mandibles from the eruption and wear of the teeth (Payne, 1973; Deniz & Payne, 1982) and his system of coding the teeth has been followed in the present work (see Fig. 1). Other systems for ageing the mandibles of goats have been devised by Bullock & Rackham and for sheep/goat by Grant (see Wilson *et al.*, 1982).

Another technique for establishing the age of an animal from its teeth, widely used in the field of wildlife management, is by counting the cementum lines in the roots. In the archaeological context it has been discussed by Koike & Ohtashi (1987) and by Stallibrass (1982) but not with specific reference to sheep. The annual deposition of cementum should be clearly visible in the Soay sheep which undergo such a regular regime of high and low nutrition. The method has not been used on the specimens in the present study but it is being carried out on a very large sample of mandibles from Soay sheep on Hirta that died after the severe winter of 1986 (T. Clutton-Brock, pers. comm.).

Criteria for sexing

Sexual dimorphism can be seen in the horns and in the skeleton of Soay sheep as in all other sheep. The ram is a considerably larger and heavier animal and the horns are nearly always much larger. Occasionally however, a ram may be found with only a scurr for a horn and this occurs frequently in the ewe. The ewes normally have either no horns or small ones. This dimorphism is reflected in the horn cores, in the skull, and in the size of the bones, as can be seen from the summaries of measurements presented in the Appendix. Further dimorphic characters can be seen in the atlas, the axis, and the pelvis. These characters were first described by Boessneck, Müller & Teichart (1964), Boessneck (1969), Gromova (1953), and Lemppenau (1964), for sheep breeds in general. They have been checked here for both the aged and sexed sample of bones and for the unknown sample. The results are shown in Figures 10–13, 22–24.

Characters of the skeleton that distinguish sheep from goat

Before the 1960's the skeletal remains of sheep and goat (apart from skulls) were not distinguished in reports on animal bones from archaeological sites. This was a grave restriction of the assessment of the economy. Subsequently criteria have been established by which most of the bones of sheep and goats can be distinguished. However these criteria have not been checked against a large collection of bones from a single population of a primitive breed. Our present study sets out to provide this check.

The characters used were first described in detail by Boessneck *et al.* (1964) and Boessneck (1969). Every feature noted by these authors as sheep-like or goat-like was checked against the relevant bones in the Soay skeletons and the feral goats from Holy Island, Arran, Scotland. However, some characters were not clearly described or were too poorly developed in the Soay bones to be defined so these were omitted from the analysis.

RESULTS

Eruption and wear of the teeth

As in all members of the family Bovidae the dental formula of the adult sheep is I: 0/3, C: 0/1, P: 2–4/2–4, M: 3/3 = 32. The lower canine is an incisiform tooth which is placed adjacent and lateral to the third incisor, leaving a long diastema between the incisor arch and the cheek teeth. The formula of the deciduous teeth is di: 0/3, dc: 0/1, dp: 2–4/2–4 = 20.

Deciduous dentition

Payne (1985) has described and illustrated the following morphological features that may be used to distinguish the mandibular milk teeth of lambs from those of kids. In the lower third deciduous premolar (deciduous molar 2 in some terminologies) of the lamb the metaconid is strongly developed and linked to the distal [posterior] part of the tooth by a short ridge running bucco-distally [labial-posterior] while in the kid this ridge connects with a more mesial part of the crown. In addition when viewed from above, the occlusal (biting) surface of this tooth is squarer than it is in the kid where it is more triangular and less robust-looking.

In the lower fourth deciduous premolar (deciduous molar 3 in some terminologies) of the lamb the crown is hypsodont with no prominent basal swelling or interlobar pillar on the buccal [labial] surface.

The cheek teeth of the yearling male, female, and castrate Soays from Hirta all complied with these characters and in no tooth were goat-like or intermediate features seen.

Permanent dentition

INCISORS. An earlier study of the dentition in living Soays, of known age, on Hirta, using portable X-ray equipment, concluded that dental development was slower than in improved breeds of sheep (Benzie & Gill, 1974). It was shown that the Soay took five to six years to reach the 'full-mouthed' stage which is characterized by the eruption of the eight permanent 'incisor' teeth to their full functional height. In improved breeds of mainland sheep in Britain this same stage is reached between three and four years according to Silver (1969) and Ryder (1983, p. 11).

In the present study the dentition of Soays of known age was examined after the death (from natural causes) of each sheep, and these field observations were later verified in the laboratory on the cleaned mandibles. In general the results of Benzie & Gill were confirmed. However, there was considerable variation of the stage of eruption amongst sheep of the same age and sex. This was most noticeable in the three year old males where eruption of the incisors ranged from the rising two-tooth stage to the rising six-tooth stage, with the majority of the animals exhibiting the four-tooth stage as might be predicted from Benzie & Gill's data.

In order to obtain comparative information on eruption of the teeth in castrated sheep the known-age wethers, held at Cambridge, were examined each year from 1978 to 1981. These castrates reached dental maturity at an earlier age. Of three wethers, three-and-a-half years old, two had attained the rising 'full-mouthed' stage, and the third had the complete set of fully-erupted incisor teeth.

All the castrates at Cambridge had reached the 'full-mouthed' stage by four years, a full year in advance of the entire males on Hirta. It would be of interest to know if the hormonal effects of castration cause early eruption of the teeth, especially as it has been claimed that the age of epiphysial fusion of the bones is, in contrast, delayed by castration. Hatting (1983) reported the early eruption of teeth in castrated, Gotlandic sheep.

CHEEK TEETH (PREMOLARS AND MOLARS). Full dental maturity is reached when all the cheek teeth are erupted and in wear, including the posterior cusp of the lower third molar. In the male and female Soays from Hirta, dental maturity occurs between the fifth and sixth years although more observations on four-year old sheep are required to establish the range fully. Again the castrates exhibited early eruption of the cheek teeth with full maturity being reached by three and a half years.

The relationship between age and the wear of the teeth in the Soays was investigated using the method devised by Payne (1973, 1987): the wear stage of the occlusal (biting) surface of each cheek tooth is defined by the pattern of the dentine, and represented by a standardized symbol as well as by a numerical code—see Figure 1. Despite the earlier eruption of the teeth in the castrates from Cambridge there are no obvious differences in the degree of wear from that on the teeth of the entire males from Hirta. Nor are there discernable differences in the wear of the teeth between the male and female sheep from Hirta.

Examination of the teeth does, however, reveal that the same state of wear can persist over a wide range of ages. This can be seen best in the lower second molar (Fig. 1d) where stage 9A is found in animals aged from 3 to 9 years. A second example is found in the lower third molar (Fig. 1e) where stage 11G is recorded in animals aged between 6 and 11 years. Finally, the very wide variation should be noted in the wear stages of the lower fourth premolar (one three-year-old with unworn cusps; others with wear up to stage 12S) and the lower third molar (stages 2A to 7G) which are recorded in the group of three-year-old males (Fig. 1b, 1e).

Skeletal pathologies

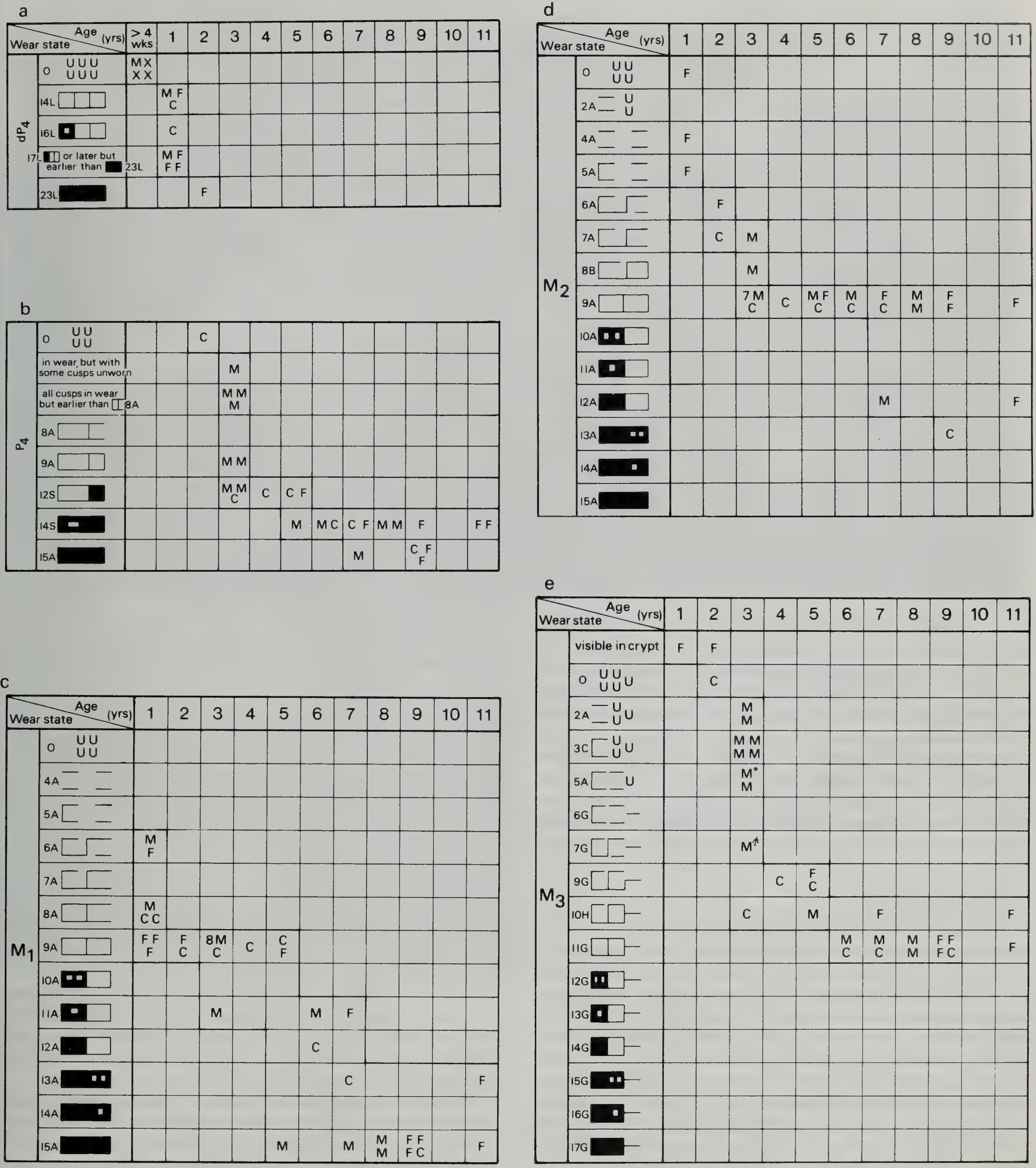
Pathological conditions are not very numerous but they are found in skeletons of all ages and of both sexes; a number are serious and must have caused considerable distress to the animals. The pathological specimens can be divided into four groups: 1 Deformities of the horn cores; 2 Anomalous teeth, periodontal disease, and abscesses on the jaws; 3 Deformities and lesions on the vertebrae and ribs resulting from trauma; 4 Tumours, abscesses, and exostoses on limb bones.

Horn cores

No pathological condition was observed on the horn cores of male sheep. However the horn cores of female sheep can respond to malnutrition or depletion of essential nutrients during breeding or lactation with a regression in growth, or loss of bone from the horn cores, producing so-called 'thumb-prints', as shown in Plate 1. Severe periodontal disease of the maxilla is also evident in this animal. 'Thumb-prints' can also be seen in both horn cores on the female skull in Plate 2. These indentations in the horn core have received little attention in the literature on osteology or pathology but have been mentioned by Hatting (1975, p. 346). They were present on the left, right, or both horn cores of eleven individuals out of a total of 50 female skulls.

Teeth and jaws

Further evidence for periodontal disease can be seen in the alveolus of the left mandibular ramus in Plate 3 at the junction of M_2 and M_3. This would have caused the animal some discomfort while the loss of all the check teeth except P^3 in the skull shown in Plate 4 would most likely have lead to the sheep's death from starvation. The right mandibular ramus in Plate 5 must be from a sheep that had a bad abscess



a

	Wear state / Age (yrs)	> 4 wks	1	2	3	4	5	6	7	8	9	10	11
dP_4	0 UUU UUU	M X X X											
	14L		M F C										
	16L		C										
	17L or later but earlier than 23L		M F F F										
	23L			F									

b

P_4	0 UU UU			C									
	in wear, but with some cusps unworn				M								
	all cusps in wear but earlier than 8A				M M M								
	8A												
	9A				M M								
	12S				M M C	C	C F						
	14S						M	M C	C F	M M	F		F F
	15A								M		C F F		

c

	Wear state / Age (yrs)	1	2	3	4	5	6	7	8	9	10	11
M_1	0 UU UU											
	4A											
	5A											
	6A	M F										
	7A											
	8A	M C C										
	9A	F F F	F C	8M C	C	C F						
	10A											
	11A			M			M	F				
	12A						C					
	13A							C				F
	14A											
	15A					M		M	M M	F F F C		F

d

	Wear state / Age (yrs)	1	2	3	4	5	6	7	8	9	10	11
M_2	0 UU UU	F										
	2A											
	4A	F										
	5A	F										
	6A		F									
	7A		C	M								
	8B			M								
	9A			7 M C	C	M F C	M C	F C	M M	F F		F
	10A											
	11A											
	12A							M				F
	13A									C		
	14A											
	15A											

e

	Wear state / Age (yrs)	1	2	3	4	5	6	7	8	9	10	11
M_3	visible in crypt	F	F									
	0 UU UUU		C									
	2A			M M								
	3C			M M M M								
	5A			M* M								
	6G											
	7G			M↑								
	9G				C	F C						
	10H			C		M		F				F
	11G						M C	M C	M M	F F F C		F
	12G											
	13G											
	14G											
	15G											
	16G											
	17G											

KEY

M	Male	C	Castrate
F	Female	X	Sex unknown

U Tooth almost at full height but unworn

— Cusps just in wear

■ Cusp worn and black indicates extent of exposure of dentine

Fig. 1 The relationship of the age in years to the state of wear on the biting surfaces of the lower (mandibular) cheek teeth of Soay sheep from Hirta. The symbols used to denote the wear patterns are those devised by Payne (1973, 1987). **a** wear over the first two years of life on deciduous premolar 4. **b** wear on premolar 4 from eruption in year 2 to year 11. **c** wear on molar 1 from eruption in year 1 to year 11. **d** molar 2 from eruption in year 1 to year 11. **e** wear on molar 3 from eruption in year 2 to year 11.

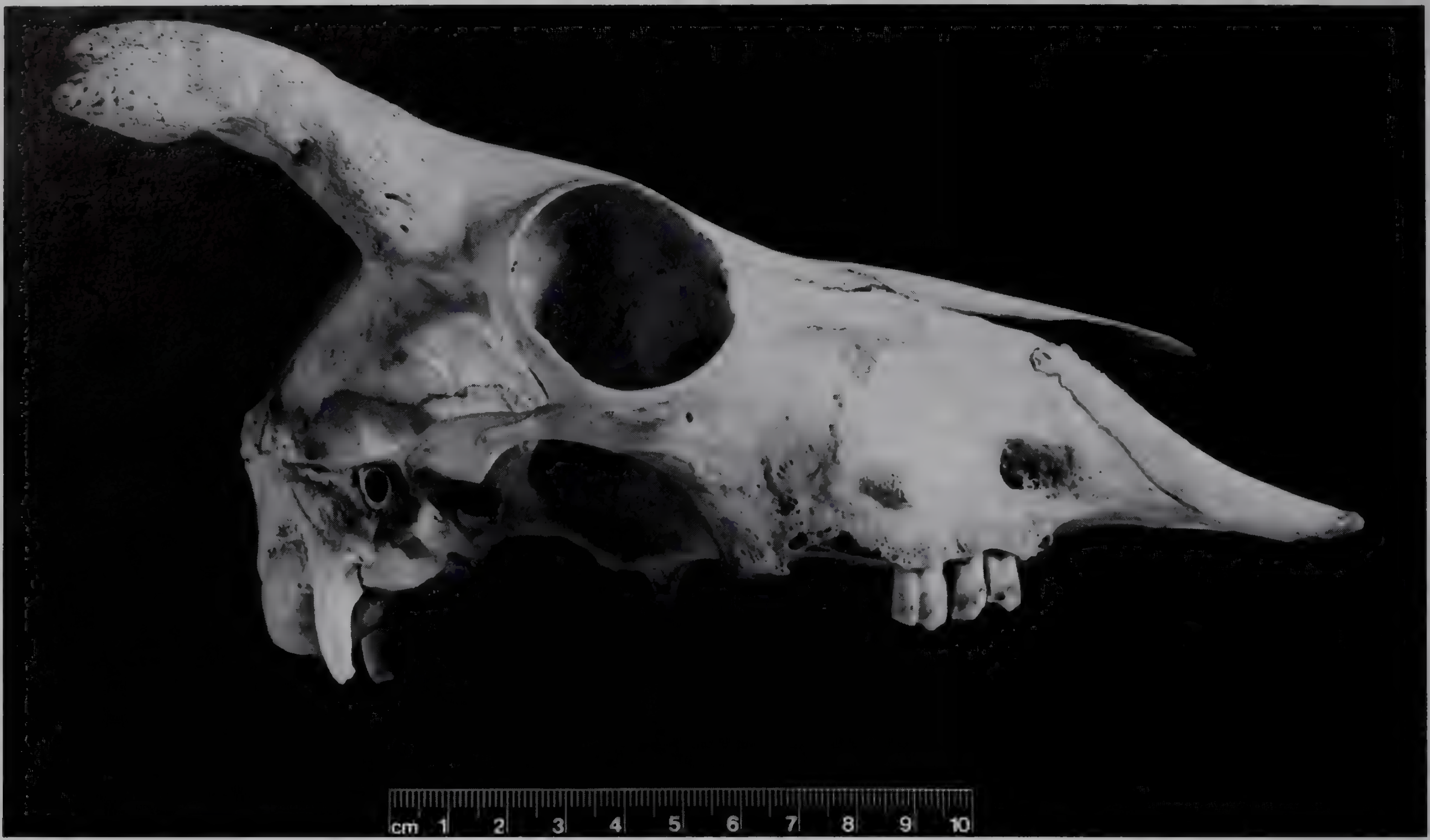


Plate 1 Right side of female skull (no. 81.931) to show 'thumb-print' on horn core and periodontal disease of the maxilla.

on its jaw, which probably began with an infection in the root of a tooth. Plate 6 shows the condyle of a mandible with extensive osteoporosis; this sheep, too, is likely to have died from starvation.

Anomalies in the growth of the teeth are illustrated in Plate 7 in which the two incisiform canines of a mandible are displaced and growing inwards, but this probably had little effect on the feeding of the sheep and the wear on the rest of the incisors and cheek teeth is normal.

Vertebrae and ribs

A common pathology in the Soay skeleton has been observed in the centra of the cervical vertebrae of male sheep. In at least one vertebra from each of 14 male skeletons from a total of 23 the posterior, cup-shaped end of the centrum is distorted, flattened, or split, as shown in Plate 8. This condition was never seen in the female. Plate 9 shows a cervical vertebra with a fracture across the anterior end of the centrum and the right transverse process. The assumption to be made from the condition of these vertebrae is that the damage is a result of fighting amongst the heavy-horned rams which batter each other's heads in shock-combat, thereby causing traumatic injury to the neck vertebrae.

The injuries do not extend to the succeeding vertebrae but in 9 out of 19 male skeletons the thoracic vertebrae show extensive ankyloses and exostoses. This is usually seen, as in Plate 10, in the skeletons of male sheep that were more than six years old when they died and the overgrowth of the bone is probably a result of an arthritic condition. In addition a number of ribs show healed fractures which could have resulted from fighting or from falls.

Plate 11 shows a posterior thoracic vertebra in which fusion has occurred between the transverse process and a rib.

There are few pathologies in the lumbar vertebrae. Plate 12 shows healed breaks on the transverse processes of three of the lumbar vertebrae from the same skeleton as the ankylosed thoracic vertebrae shown in Plate 10. This was an 8 year old male sheep that may have suffered from injuries from a fall or from fighting, as well as developing osteoarthritis in old age.

Limb bones

It is noteworthy that for animals living on steep, rocky terrain there are very few breaks in the limb bones but most of our sample was collected in the relatively sheltered village area. There is one broken metacarpal bone shown in posterior view in Plate 13. The shaft of the bone had broken across diagonally just below the proximal epiphysis and had failed to heal without infection. This caused substantial exostosis and displacement of the two ends of the shaft so that the sheep was probably lame but could have lived a normal life.

The most common pathological condition seen in the Soay limb bones is described in Baker & Brothwell (1980) as 'pen elbow'. These authors claim that, 'shepherds who recognize the condition consider that it is due to trauma to this relatively exposed site when the animals are put through races or pens. Sometimes it is associated with fractures of the olecranon'. The examples in the Soay specimens are typical in having an extra growth of bone or 'lipping' at the lateral edge of the articular surfaces of the humerus and radius, as shown in Plate 14, and exostoses around the joint which reduces its mobility: 37 out of a total of 162 radii show this condition. The articular end of the humerus in Plate 14 also has an extra 'lip' of bone on the medial side.

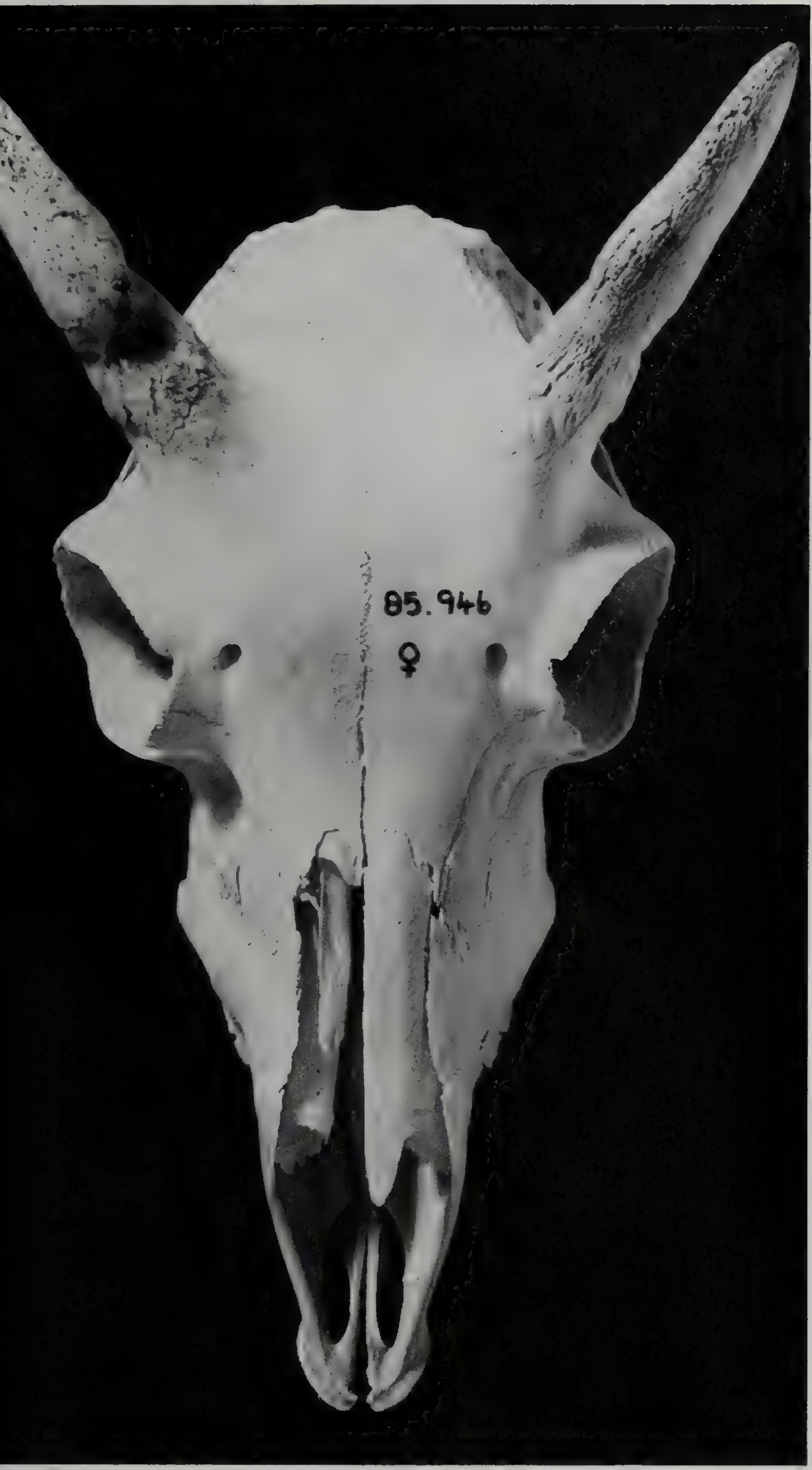


Plate 2 Female skull (no. 85.946) to show 'thumbprints' and depletion of the bone of both horn cores.

The Soay sheep on Hirta have never been penned or driven by humans but it is possible that injury to the elbow joint occurs when the sheep crowd together in the cleits.

Plate 15 shows a humerus with a severely deformed distal epiphysis. There is extensive overgrowth of the bone and an eburnation on the medial condyle which is typical of osteoarthritis, as described by Baker & Brothwell (1980).

Radiographic examination of skeletal elements

Although there are some severe pathologies in the bones of the Soays, in general the skeletons appear to be from healthy animals that show little evidence of malnutrition. This agrees with the findings of Benzie & Gill (1974) who made a radiographic survey of 50 living sheep on Hirta in 1965 and 1966. They concluded that the mineral status of the skeleton of the Soay sheep on the island was good and could compare favourably with mainland sheep grazing on a good hill.

In the present study a series of femora and other limb bones were radiographed in an attempt to identify Harris's lines. These horizontal lines, which reflect a period of retarded growth, can sometimes be seen at the ends of long bones and in the mandible in skeletons of animals or humans that have undergone a period of starvation or stress (Mays, 1985; Baker & Brothwell, 1980). No Harris's lines or evidence of starvation were seen in the radiographs of the Soay bones.

Radiographs of the metapodial bones of the Soays were used by Liora Horwitz to assess the effects of lactation on the thickness of cortical bone relative to the width of the medullary cavity. Horwitz found that the cortical bone of the metacarpals of the female Soays from Hirta was slightly, but significantly, thinner than that of metacarpal bones of female Soays from Babraham, Cambridge, which had been on a uniformly higher plane of nutrition. There was no difference in the cortical thickness of the metacarpal bones of rams from Hirta and Babraham (Horwitz, pers. comm.) However, this thinning of the cortical bone, which results from loss of calcium during lactation, does not appear to have a detrimental effect on the health of the ewes which normally live considerably longer than the rams.

Castrates

The castration of male lambs has been an important part of agricultural practice for thousands of years, with beginnings perhaps as early as the Neolithic period. As every farmer knows, castration causes the lamb, or wether, to grow larger, fatten earlier, and develop a finer fleece. As the Soay sheep on Hirta had been living as a feral population no castration had been carried out in recent times until 1978 when a number of lambs were castrated in order to compare their development and behaviour with that of the rams. These castrates were still alive when the skeletons for the present study were collected, with the exception of two one-year olds which have been included: seven castrates of known age, shown in Table 1, were obtained from the flock of Hirta Soays maintained in Cambridge (see Materials and Methods).

There is some evidence to suggest that castration causes a delay in the time of fusion of the epiphyses of the bones (eg., see Brännäng, 1971; Noddle, 1974), leading to an extension of the period of growth so that castrates are taller animals than the entire males. This theory could not be checked on the castrated Soays because there is no three year old skeleton to compare with the entire males, the bones of which were at the crucial stage of fusion as shown in Figure 2. The bones of the castrate aged three years and five months are all fully fused, indicating that at least in this sheep fusion was not greatly delayed.

Hammond (1940, p. 85) claimed that castration reduces the 'thickness' (ie., the width of the shaft) of the limb bones to that found in the female. The measurements of the Soay castrates (see Appendix) do not show any significant reduction in shaft width over that of other males but it can be seen from Table 2 that their bones are nearly all considerably longer. This increase in length is unlikely to be the result of a higher plane of nutrition in the mainland sheep because, as can be seen from Table 3, the lengths of the limb bones of

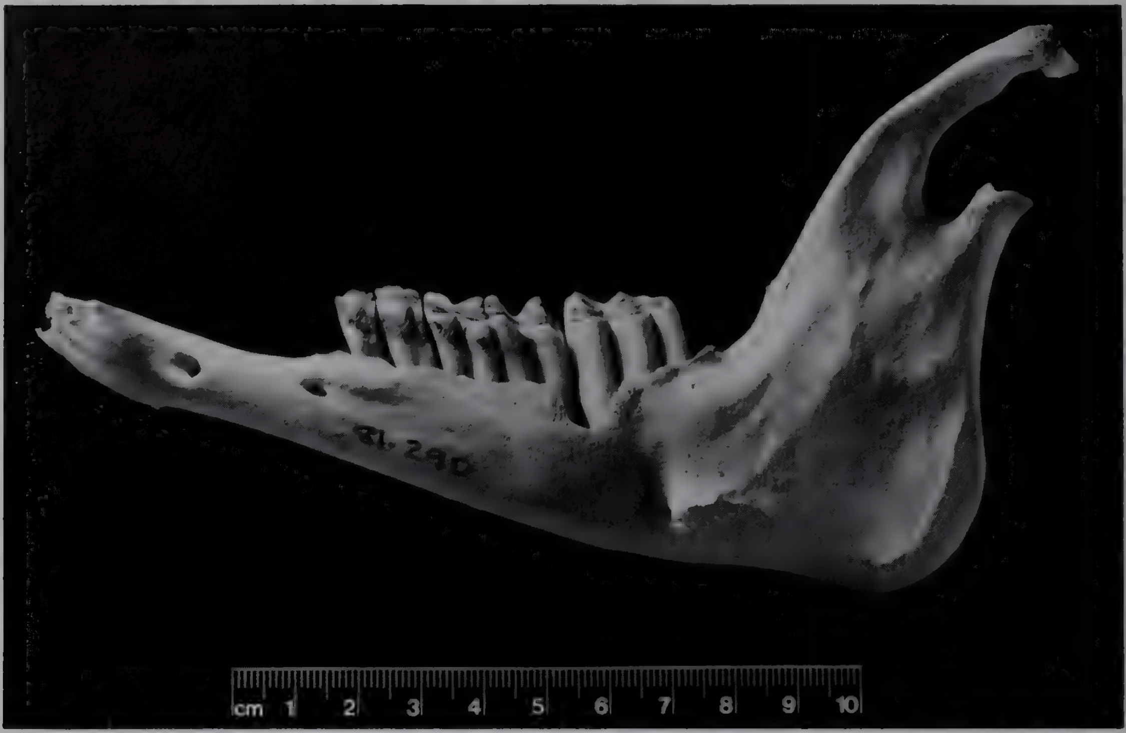


Plate 3 Left mandibular ramus (no. 81.290), female, to show periodontal disease.

male sheep from Babraham fall within the same range as those of the male Soays from Hirta (compare Tables with Appendix). It is much more likely that the hormonal changes brought about by removal of the testes leads to a lengthening in the period of growth. Why this should be greatest in the extremities of the skeleton is not known but the measurements show that the facial region of the skull and the lower limb bones are most affected.

Growth, form, and inheritance of the horns and horn cores

Male horns

As in all sheep and goats, the horns of the Soay ram are adapted for use in intraspecific fighting, in which rival males engage in horn-to-horn butting (crashing their horns head-on after running towards each other). Such encounters are often fierce and the horns are therefore strongly developed in the adult, and even as early as one year Soay males have begun to develop short, stout horns (Fig. 3).

By three years of age the male Soay exhibits the typical adult horn conformation; each horn curves outwards and backwards spiralling round the ears, with the tip pointed forward. Although there is a slowing down in the annual incremental growth, male horns continue to increase in length well into old age. This situation may be contrasted with the noticeable plateau in the growth rate that is a feature of horns in the female Soay beyond 5 to 6 years of age (Fig. 3).

Viewed in cross-section, the bases of both the sheath and core in the adult male horn are D-shaped, with the anterior edge more rounded and broader than the tapered, posterior edge (Fig. 4). This broad anterior edge confers strength on the horn; as discussed by Schaffer & Reed (1972, p. 48–51) and Kitchener (1985, p. 191) it is precisely this basal area that receives and must be capable of withstanding the full brunt of the force of impact during butting. Additional strength for the horn comes from the solid construction of the core. Studies of male and female horn cores by X-rays reveal that in the male the sinus (or internal cavity) is restricted to the basal area whereas in females it occupies up to one half of the total volume and is surrounded by very much thinner walls than in the male (Fig. 5). One of the effects of castration is seen in the extension of the sinus, resulting, in some individuals, in an almost hollow core (Fig. 5).

Compared with the fierce intraspecific fights staged between male sheep, the antagonistic behaviour in male goats is generally less violent and takes the form of rivals clashing their horns, often crossing them at the moment of impact, with the force of impact delivered at a much higher point along the horn's length (see Schaffer & Reed, 1972, Fig. 23, p. 48). As they do not have to withstand such high impact forces, the horns of goats are 'relatively and absolutely more narrow than those of . . . *Ovis*' (ibid, p. 50). Also in goats the horn bases are located further back on the skull and are closer together than in sheep; and irrespective of whether the horns are straight or twisted (depending on breed) the horns of goats are usually more upright than in sheep where part of the horn lies below the dorsal level of the skull.

As in other members of the Caprini (see Kiltie, 1985, p. 316) male Soays show remarkably little variation in horn conformation; and—apart from the occasional incidence of scurred or crumpled (ie. deformed or rudimentary) horned rams—the majority of males within each age group have very similar horn development with only minor differences in size associated with differences in body weights. This conformity is demonstrated by the relatively low coefficients of variation in the lengths of horn sheath of the male yearlings and three year olds on Hirta, in 1979 (Table 4). The 1979 material included a two-year old ram with stunted horns which were short and conical in form, with a circular cross-section at the base. The three-year old group also included one individual male with very reduced sized horns whose presence 'artificially' increased the calculated value of the coefficient of variation in that group (see Table 4). No examples of polled rams were recorded in 1979/80.

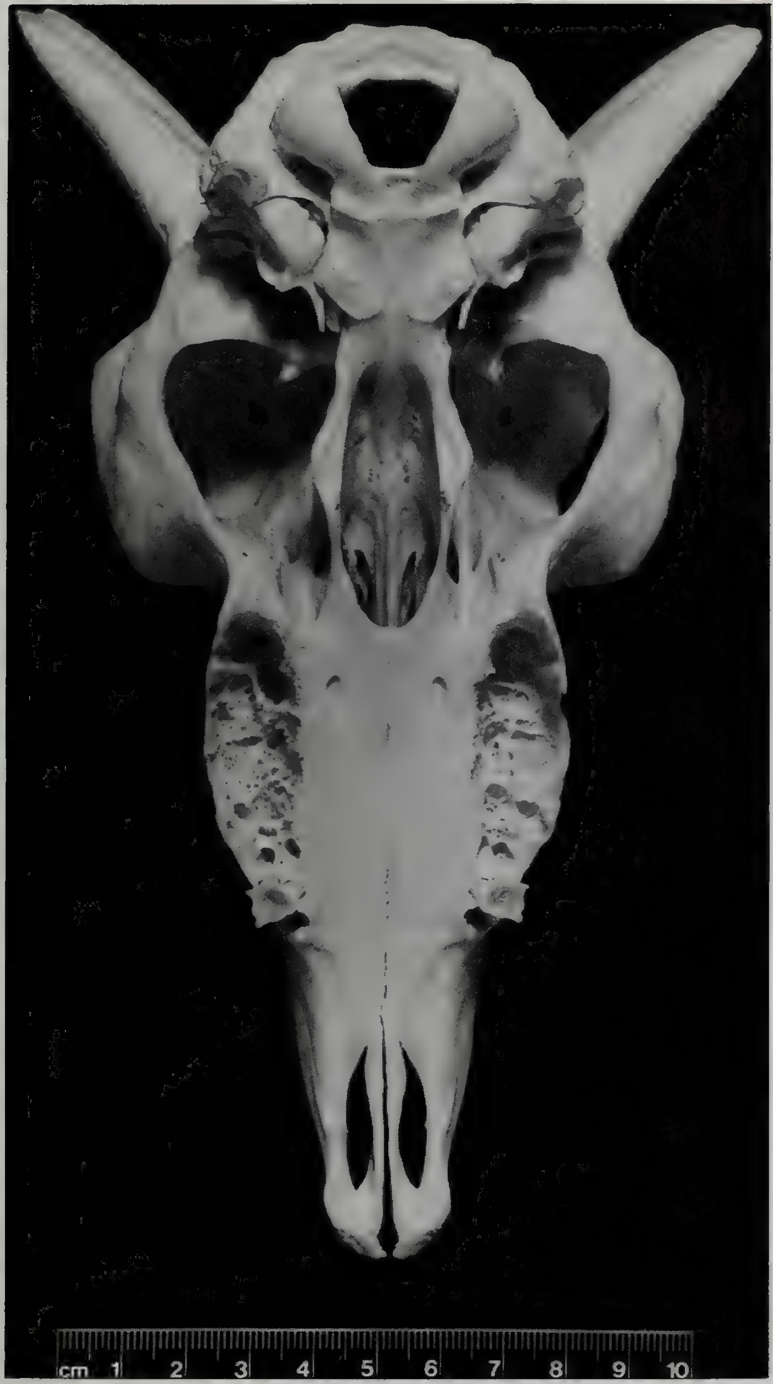


Plate 4 Palatal view of skull (no. 81.1719), female, to show loss, during life, of all the cheek teeth except the third premolars, probably a result of extensive periodontal disease of the maxillae.

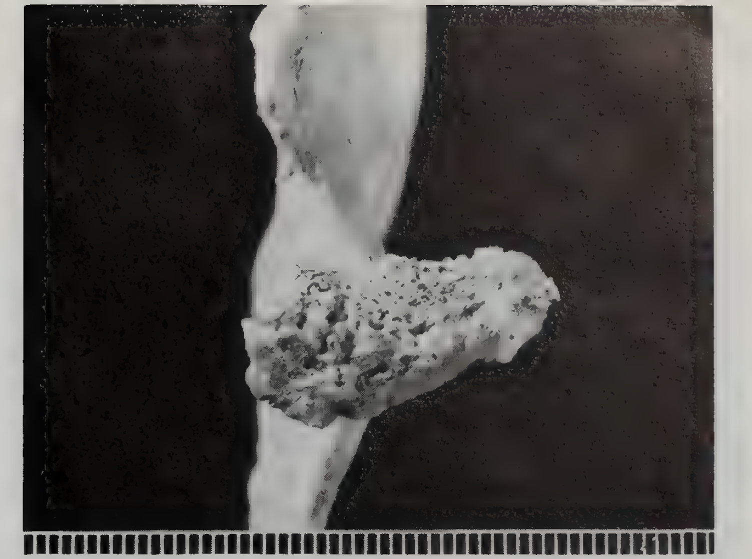


Plate 6 Left condyle of mandible (no. 87.1180) to show extensive osteoporosis. The right condyle is in a similar condition.

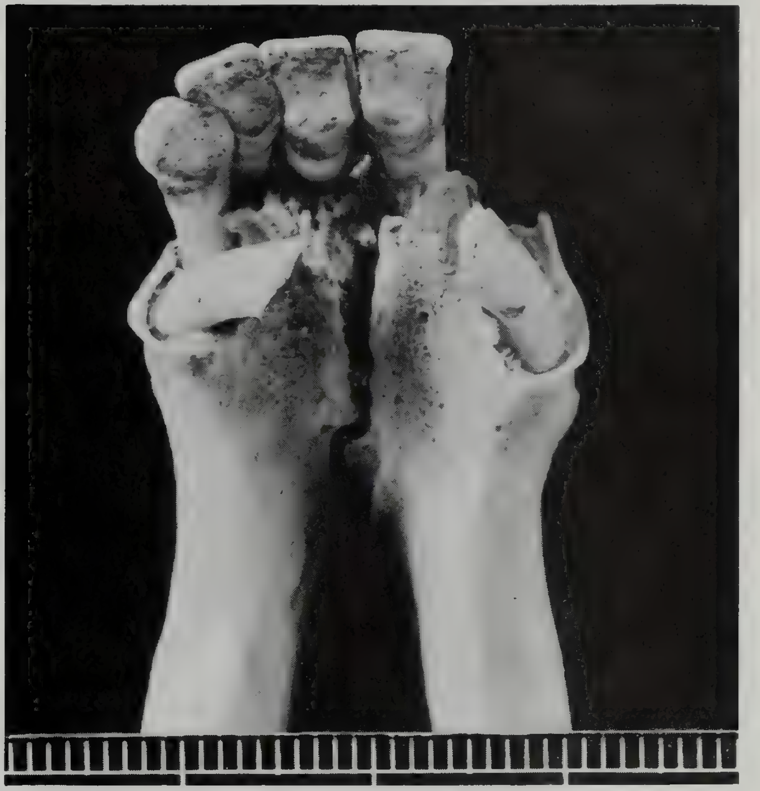


Plate 7 Symphysial region of mandible (no. 87.1179) to show the anomalous position of the incisiform canines which are growing inwards.

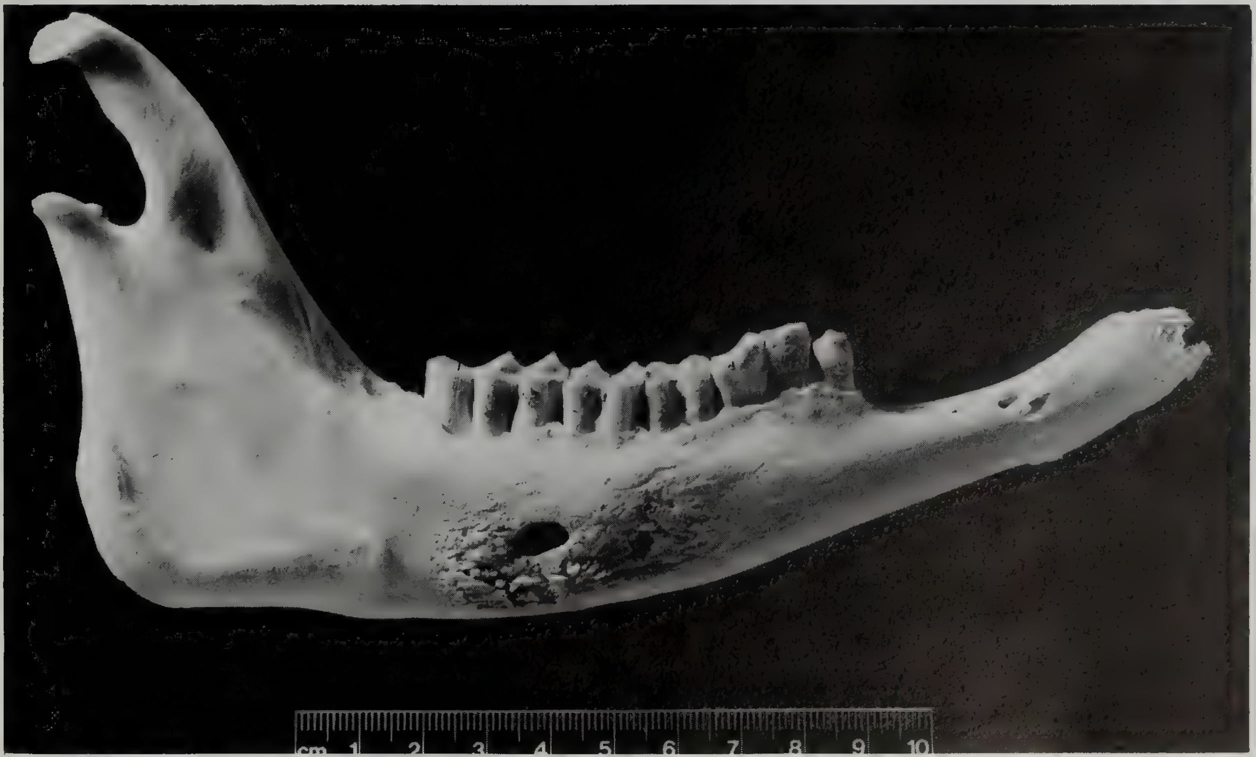


Plate 5 Lateral side of right mandibular ramus (no. 78.1883) to show abscess, probably formed at the roots of M_2 and M_3.

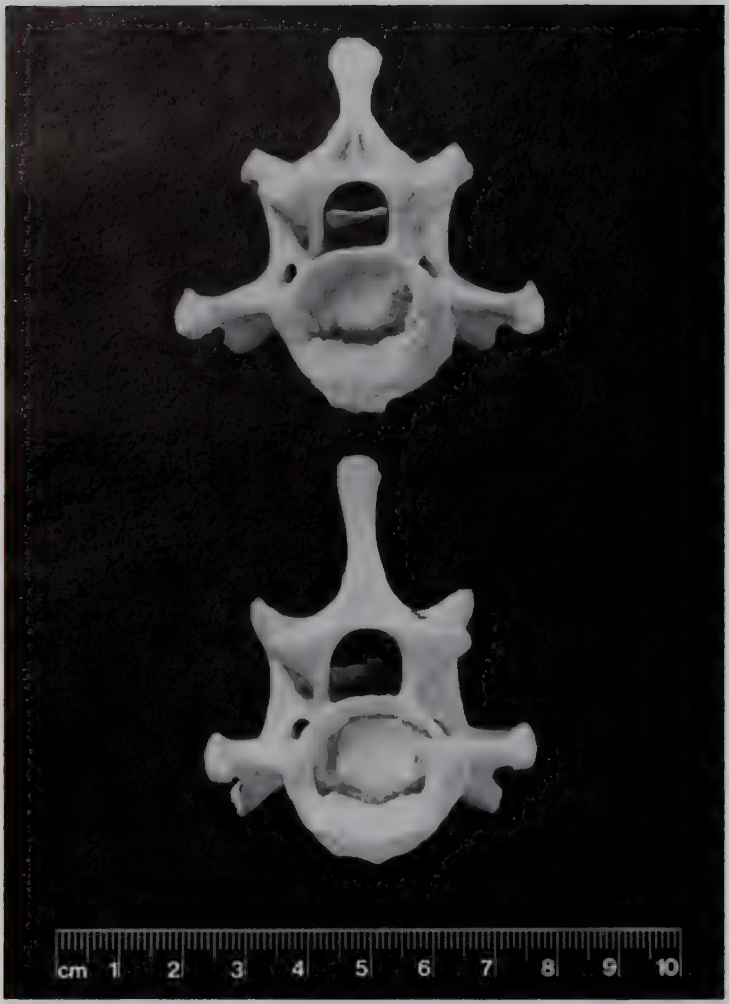


Plate 8 Posterior views of cervical vertebrae (no. 1963.12.17.1), male, to show damage to the centra.

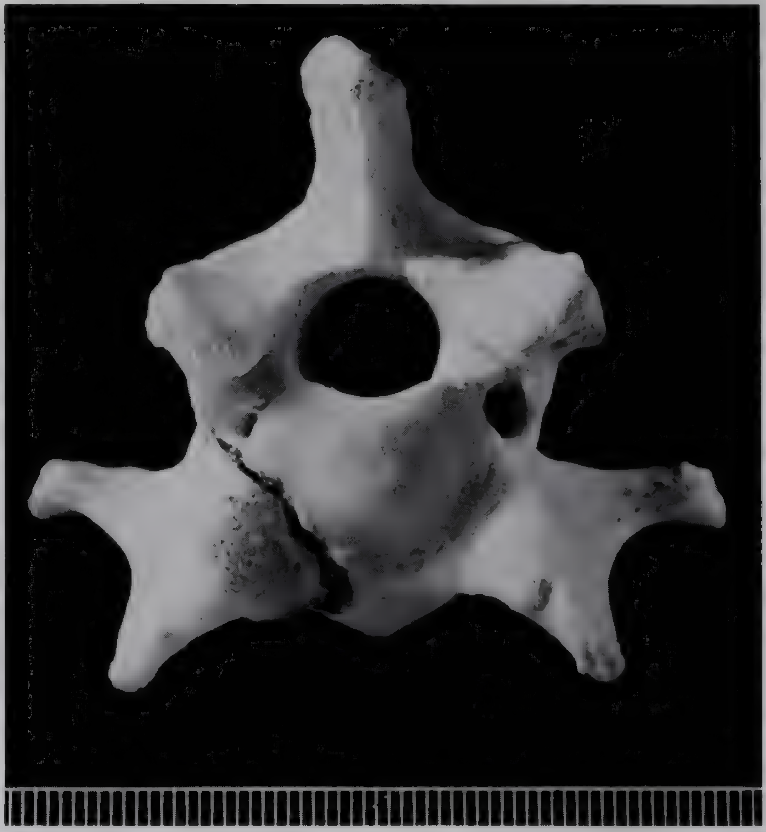


Plate 9 Anterior view of cervical vertebra (no. 78.1633), male, to show the fracture of the centrum and transverse process.

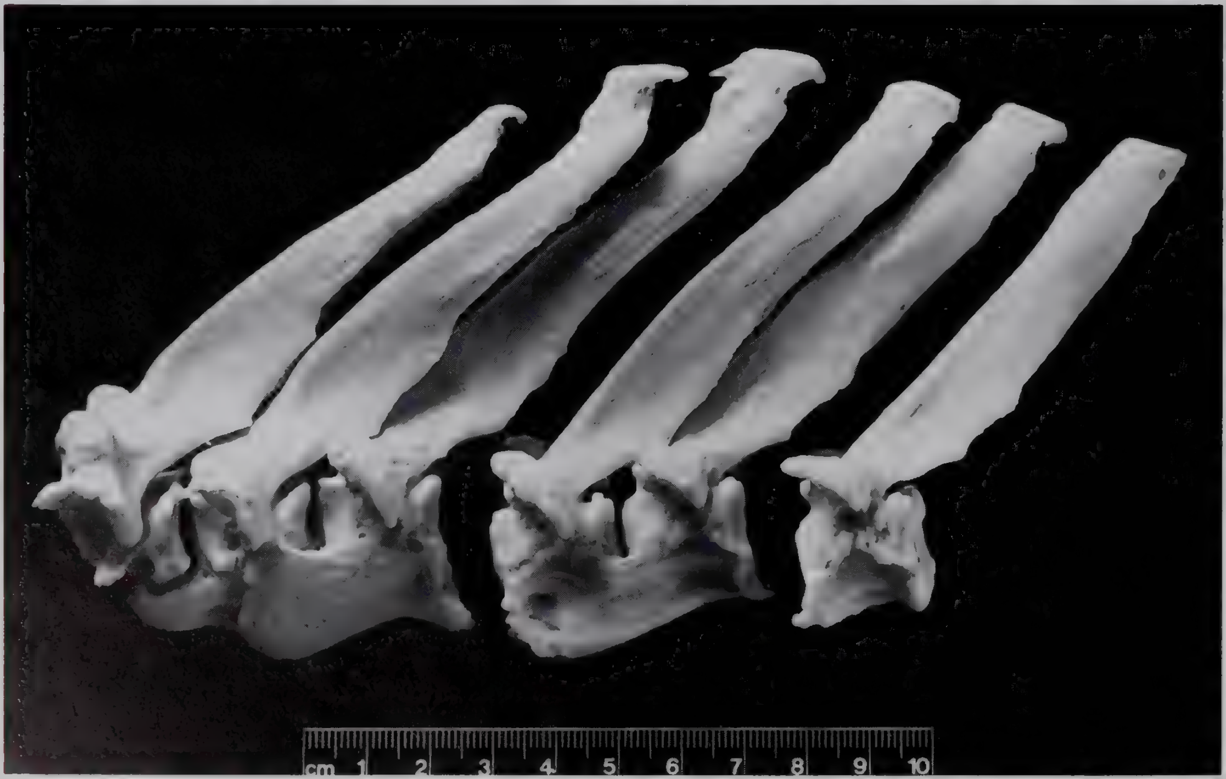


Plate 10 Lateral view of right side of thoracic vertebrae (no. 85.947), male, to show ankyloses.

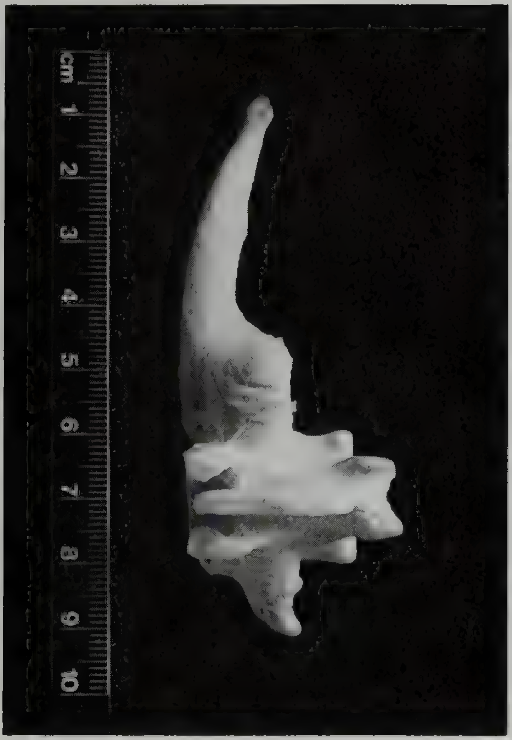


Plate 11 Dorsal view of 13th thoracic vertebra (no. 1981.1773), male, to show fusion of the transverse process with a rib.

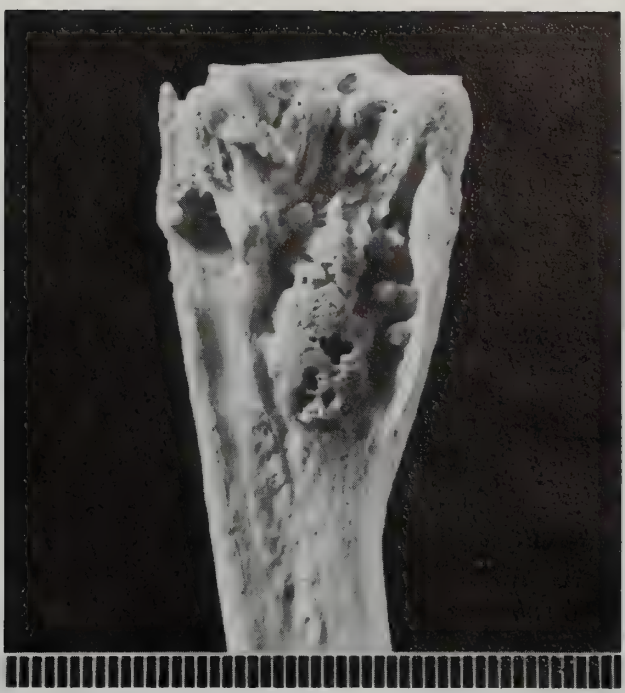


Plate 13 Posterior view of proximal end of metacarpal bone (no. 78.1896) to show exostosis of the bone as a result of a fracture of the shaft.

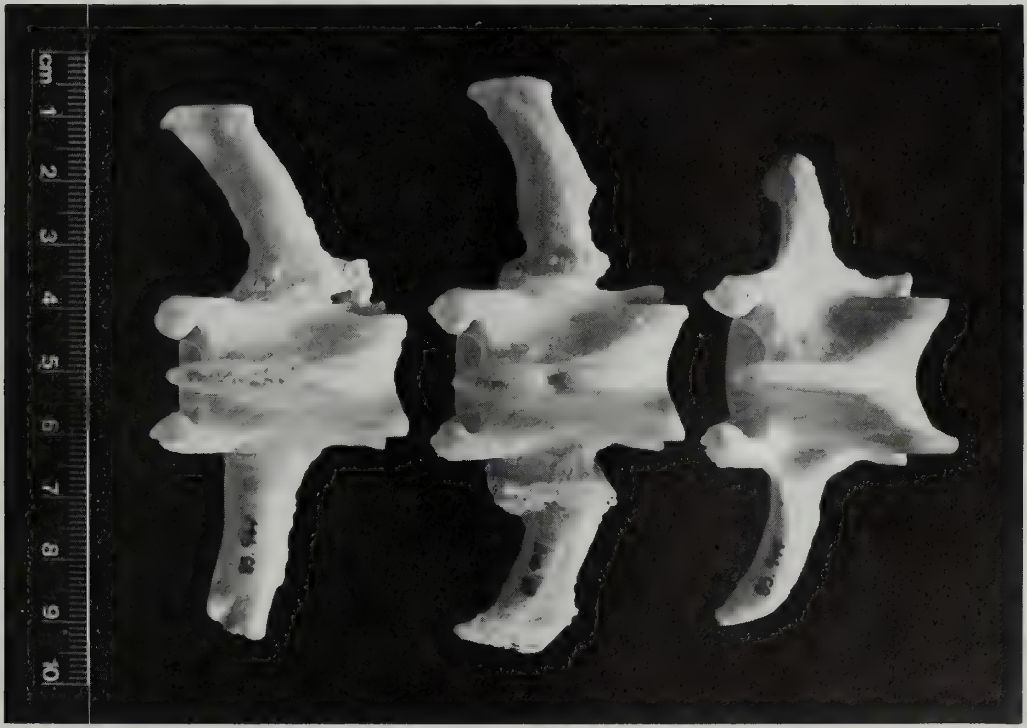


Plate 12 Dorsal view of lumbar vertebrae (no. 85.947 the same skeleton as the vertebrae in Plate 10) to show healed fractures on the transverse processes.

Female horns

Previous workers have been content to assign the island ewes to the two groups, horned and polled. The present study shows that this is too simple an approach and that the horned and so-called polled conditions are in reality the extremes in a range of conditions, covering a continuum of horn and horn-like structures. Accordingly, it was decided to classify the Soay ewes using the system of Kelley (1951) which recognizes the existence of knobs and scurs as well as the fully horned condition (ibid, p. 10). Under this scheme it should be noted that the truly hornless state is characterized by concave depressions or smooth (level) surfaces at the horn sites.

A measure of the very wide range in forms of horn and scurs in the female Soays on Hirta is the extraordinarily high value (48.2) of the coefficient of variation of horn sheaths of yearling ewes (see Table 4) which fits very well the observations made by Kiltie (1985, p. 315–17).

Plots of the length of the hornsheaths from known-age Soay ewes reveal the very different growth pattern compared

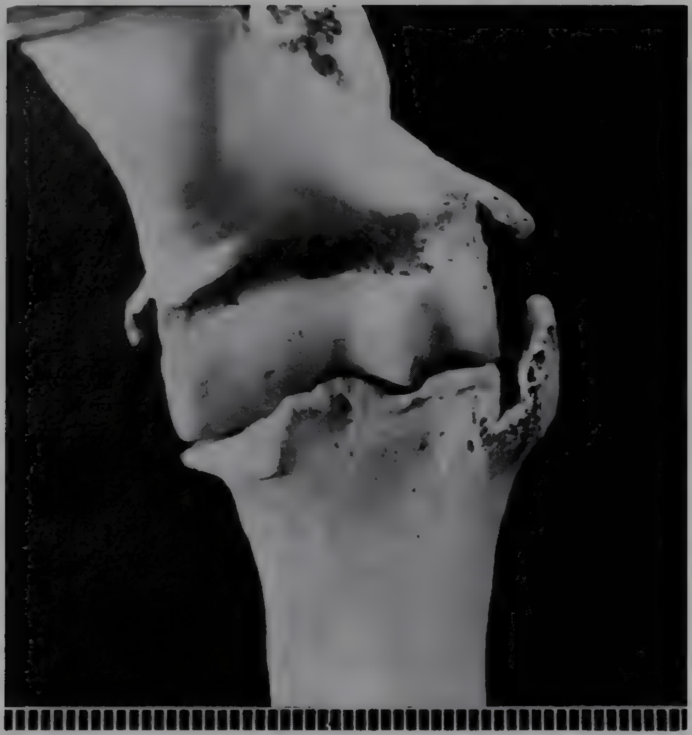


Plate 14 Anterior view of left elbow joint (no. 82.706) to show 'pen elbow', a condition in which there is extra growth of bone, or 'lipping' on the medial and lateral edges of the distal epiphysis of the humerus and on the lateral edge of the proximal epiphysis of the radius.

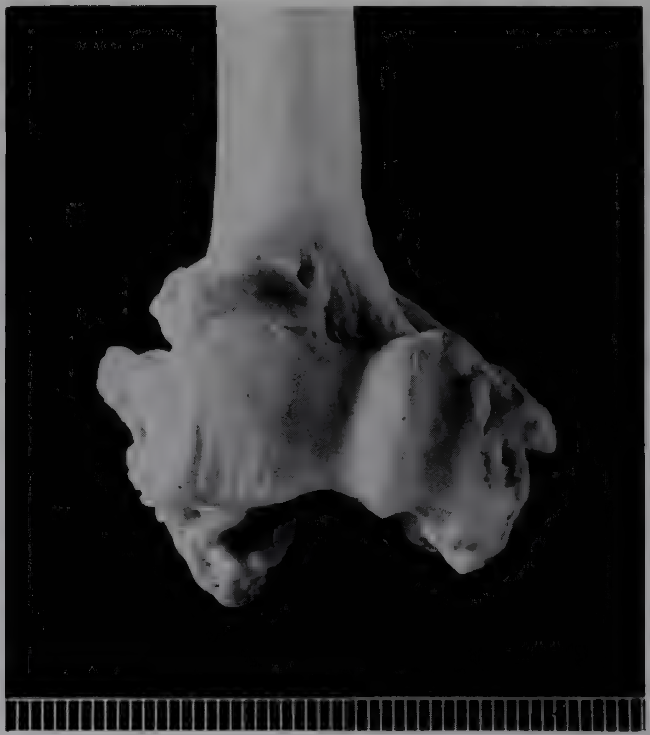


Plate 15 Anterior view of distal end of left humerus (no. 78.1893) to show osteoarthritis, exemplified by gross exostosis and eburnation of the medial condyle.

Table 1 Data on the castrates

Reg. no	Killed	Age	Withers height (live) cm	Weight Kg (live)	Metacarpal length* cm
81.1760	May 81	2yr1m	58	24.2	118.9
82.574	Oct 81	3yr5m	66	36.2	130.4
81.1759	May 81	4yr	61	30.2	129.5
84.795	Mar 84	4yr11m	67	36.0	123.2
81.1758	May 81	6yr1m	68	38.0	131.5
84.796	Mar 84	6yr10m	71	39.0	134.6
84.794	Mar 84	8yr11m	67	32.0	127.7
The castrate skeleton from Babraham					
76.1841		6yr4m			124.5

* Measured from the prepared skeleton

Table 2 Percentage differences between the mean lengths of the bones of the entire male Soays and the castrates.

Element	Castrate longer than male	Entire male longer than castrate
	%	%
Skull	11.28	–
Mandible	12.78	–
Atlas	–	1.07
Axis	–	3.70
Scapula	9.88	–
Humerus	3.20	–
Radius	8.00	–
Ulna (length olecranon)	7.50	–
Metacarpal	6.30	–
Innominate	–	.64
Femur	4.70	–
Tibia	8.00	–
Patella	–	2.80
Talus	.11	–
Calcaneum	4.50	–
Metatarsal	9.26	–
Phalanx 1	1.80	–
Phalanx 2	–	.81
Phalanx 3	8.39	–

with that documented for Soay rams (Fig. 3). Unlike the male, there is no rapid rate of growth in the first three years, but a steady and gradual increase in the growth rate until the 5th or 6th year after which there is only minor annual incremental growth. Throughout life the pace of horn development is much slower than in the male, and the adult female horns in consequence are far less robust and much shorter. The fully developed female horn in the Soay breed is reminiscent of the female goat horn in that both have sharp keel-shaped anterior and posterior edges and are generally flattened medio-laterally; the tip of the horn in the Soay ewe, however, is much more rounded (blunt-ended) than in the goat where it has a sharp, pointed tip.

Effects of castration on the horns

Castration of horned Soay rams within a few days of birth retards the rapid initial growth phase that is characteristic of the entire male (Fig. 3); instead the horns develop very much like those of the female but are somewhat more heavily-built and longer (Figs 4 & 5).

Nordby (1928) recorded a similar retardation in horn development in Rambouillet ram lambs castrated at an early age, and in Merinos, where the males only are horned (the females being either hornless or scurred), castration produced an animal that remained hornless. In field observations made in 1980, on Hirta, it was seen that only those ewes that

BONE / AGE (years)	Humerus						Ulna			Radius			Metacarpal		
	prox.			dist.			prox.			dist.			dist.		
sex	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C
new born	u			u			u			u			u		
1	2 u	u	2 u	2 ●	●	2 ●	2 u	3 u	2 u	2 u	2 u	2 u	2 u	3 u	u
2yr 1mth			u			●			u			u			u
3	4 u 3 ○ ⊘ ●	●̸		9 ●	●		2 u 4 ●̸ 3 ●			7 u ○ ⊘	●		2 u ○ 4 ⊘ 2 ●		
3yr 5mth			●			●			●			●			●
4			●			●			●			●			●
5	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	2 ●	●

KEY

u	unfused
○	beginning to fuse
⊘	part fused
●̸	almost fused
●	fused
M	male
F	female
C	castrate

BONE / AGE (years)	Femur						Tibia						Metatarsal			Calcaneum			Phalanx 1			Phalanx 2		
	prox.			dist.			prox.			dist.			dist.			prox.			prox.			prox.		
sex	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C
new born	u			u			u			u			u			u			u			u		
1	2 u	2 u	2 u	2 u	2 u	2 u	2 u	u	2 u	2 u	u	2 u	2 u	3 u	2 u	2 u		2 u	2 u		u ○	u ⊘		u ○
2yr 1mth			u			u		u	u		u	●			u			●			●			●
3	3 u 4 ⊘ ●̸ ●	●		6 u 2 ○ ●	●̸		7 u ○ ●̸	●̸		●̸ 8 ●	●		2 u 4 ⊘ ●			2 u ●̸ 3 ●			7 ●			4 ●		
3yr 5mth			●			●			●			●			●			●			●			●
4			●			●			●			●			●			●			●			●
5	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	●	●	●	●	●	●	●	●

Fig. 2a & b The states of fusion of the proximal and distal epiphyses of the limb bones of Soay sheep of known ages up to five years. The number in front of each symbol (see key) indicates the number of invidivuals in that category.

Table 3 Length measurements (mm) of limb bones from five male skeletons of Soay sheep bred at Babraham, Cambridge.

HUMERUS			
	length of bone	max	139.3
		min	129.9
		mean	136.16
		st. dev	3.63
RADIUS			
	length of bone	max	151.6
		min	139.7
		mean	147.36
		st.dev	4.58
METACARPAL			
	length of bone	max	124.4
		min	111.5
		mean	119.04
		st.dev	5.03
FEMUR			
	length of bone	max	170.5
		min	158.6
		mean	165.58
		st.dev	4.97
TIBIA			
	length of bone	max	204.6
		min	189.2
		mean	199.18
		st.dev	6.59
METATARSAL			
	length of bone	max	136.7
		min	123.2
		mean	130.18
		st.dev	5.04

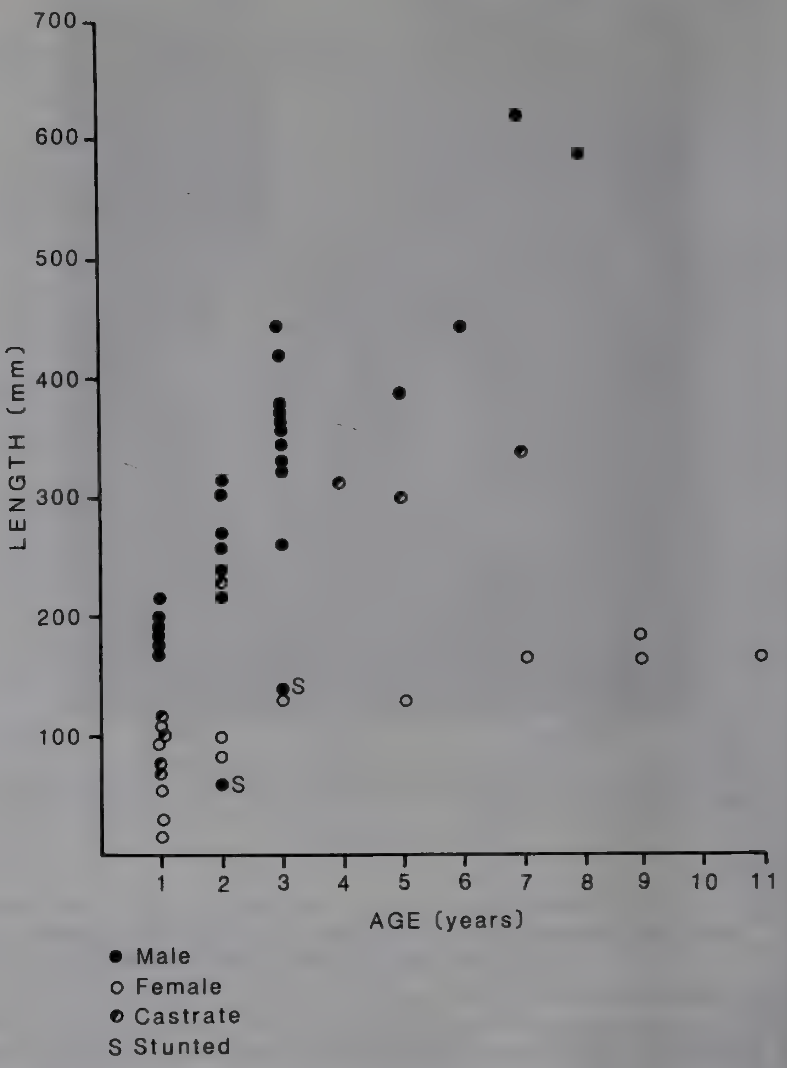


Fig. 3 Horn sheaths of male, female, and castrated Soay sheep. The length of the horn is plotted against the age of the sheep in years.

appeared to be hornless produced lambs that grew into polled castrates—conversely, castrated ram lambs of horned ewes all developed horns (Hatting, 1975, 1983 reported similar effects in castrated Gotlandic and Faroese sheep, and see section on horn inheritance, below). It was, however, not possible to ascertain whether those castrates classified as polled were truly hornless or whether some of them had knobs at the horn sites.

The inheritance of horns

The study of horn inheritance in the Soay is difficult because of the considerable variety of horned condition in the ewes. In an earlier study, Doney *et al.* (1974) classified Soay ewes according to the broad categories: horned and 'polled' (including scurred); thereby eliminating the complication of trying to explain the very wide variety of horn and horn-like structures in females. They were able to demonstrate that the phenotypic frequencies followed the Hardy-Weinberg law, based on the assumption that hornedness is controlled by an allele dominant to the one for hornlessness. They acknowledge that horn inheritance in the Soay is probably more complex than this (Doney *et al.*, 1974, p. 98).

The visit to Hirta by P. L. Armitage in August 1980 provided a good opportunity to investigate further this problem. August proved to be an ideal time for such a study as the first phase of horn growth in the lambs was then virtually completed. Moreover, as the lambs had not yet been weaned, it was possible from field observation using binoculars to determine whether or not their dams were horned or polled. It was not possible to distinguish between the truly hornless (clean polled) individuals and those with very small, inconspicuous knobs; and in consequence the data relating to polled sheep include both conditions. Sheep with well developed scurs or stunted/deformed horns were, however, identified and recorded in a separate category from the horned group. The sex of individual lambs was manifest from the colour and arrangement of the ear tags. The data collected are summarised in Tables 5 and 6.

From the collected data the following general 'rules' of horn inheritance in the Soay may be suggested:

1. Irrespective of whether the dam is horned or polled virtually all entire ram lambs are horned and the only example of a scurred male lamb was the progeny of a polled ewe.
2. Polled ewes produce proportionately more polled female lambs than horned.
3. Horned ewes produce proportionately more horned female lambs than polled, and this is true also of those ewes with scurs or stunted horn-like organs.
4. With the exception of a single horned castrate, all of the castrates from polled dams are also polled.
5. With the exception of a single polled female, all of the offspring (irrespective of whether male, female or castrate) of ewes with either scurs or stunted horns are horned.

Apart from the brief analysis published by Doney *et al.* (1974, p. 98) we know of no other study that attempts to explain the

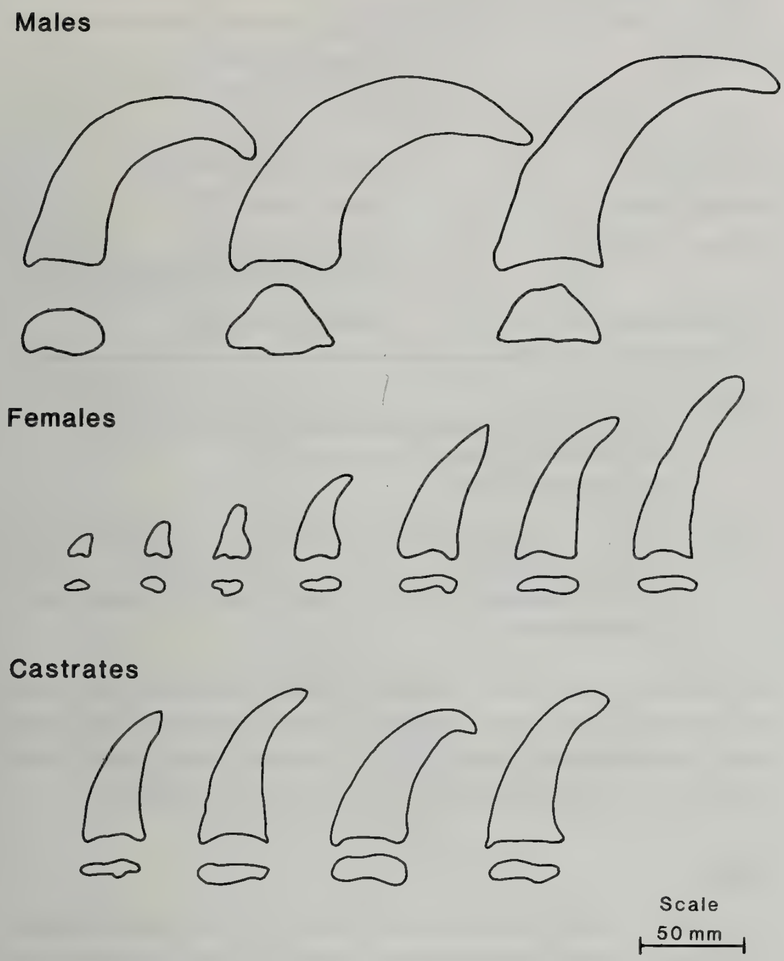


Fig. 4 Horn sheaths of Soay sheep (collected from Hirta in 1979). The lateral profiles and basal shapes have been traced to show the variation in horns of yearling females (top), males (middle), and castrates (bottom).

genetic mechanisms governing horn inheritance in the Soay, despite the appearance of over 200 papers on sheep horns between 1811 and 1981 (see Font *et al.*, 1982). In the absence of any direct investigation of the Soay, the results of work carried out on Merino, Rambouillet and Merino-type sheep are perhaps the most relevant to an understanding of the genetic mechanisms in the Hirta sheep, as in these breeds males are horned and females either polled or have knobs or scurs. A summary of the theories postulated for these breeds is given in Rae (1956): the most plausible theory involved the presence of polygenes that modify the action of the major gene(s) governing the horned and polled conditions. In this way a number of minor (non-allelic) genes (polygenes) influence the expression of the major gene(s) through epistatic and/or hypostatic interactions to produce the observed range of continuous variation 'which has maximal horn-growth and the most concave depressions as its two extremes' (Kelley, 1951).

Although Kelley's theory fits very well the observed evidence for the Soay sheep, he fails to provide any appropriate symbols designating the polygenes; and it is therefore necessary to adopt those used by Ibsen & Cox (1940) and Ibsen (1944) in order to construct a tentative model illustrating the genetic basis of the various conditions recorded in the Soay sheep (see Table 7).

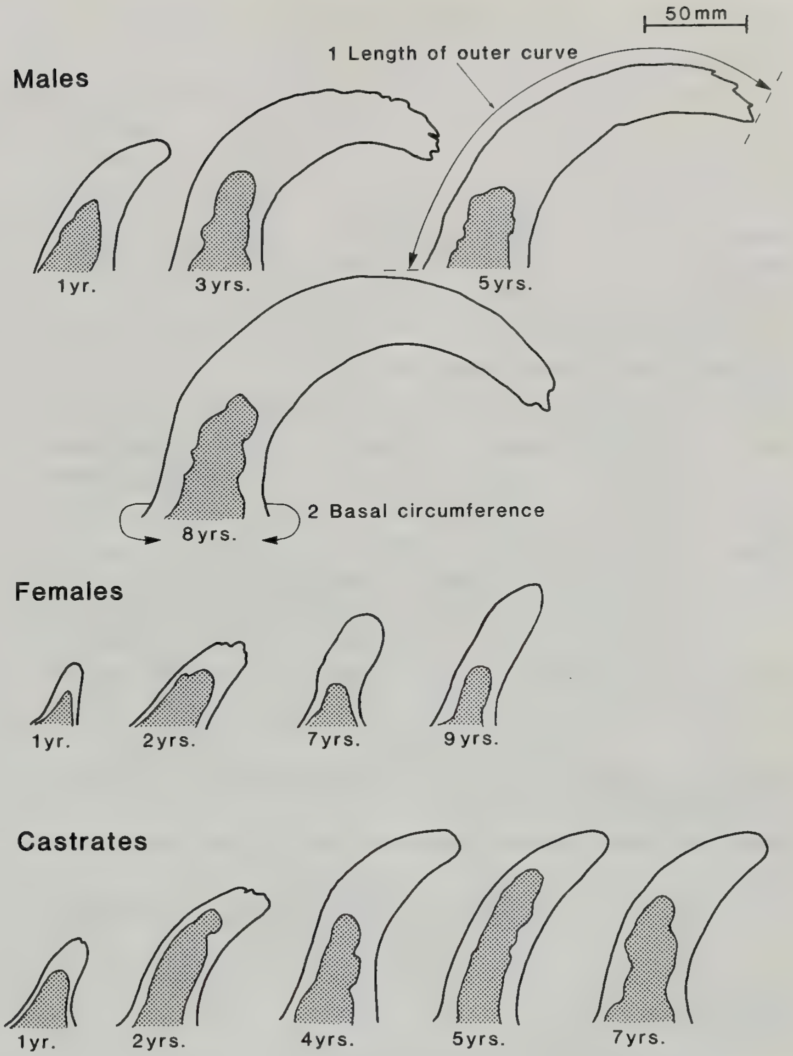


Fig. 5 Tracings of radiographs of the horn cores of male, female, and castrated Soay sheep at different ages to show the location and extent of the sinus (cavity). 1 and 2 measurements (see Appendix).

Description of the skeletal elements and analysis of sheep-like and goat-like characters in the Soay

A system of scoring was devised so that each character was recorded as sheep-like, goat-like, or intermediate between sheep and goat. (A fourth score of anomalous was deleted from the final results as it included so few elements). Every character was visually tested on the Soay skeletons and on the bones of the feral goats from Holy Island, but scores were only analysed from the sheep bones.

The results of the analysis are presented as block diagrams for each character investigated for each element; these readily reveal which characters are diagnostic of sheep, which are closer to the goat pattern, and which are intermediate. The vertical axis in the diagrams gives the numbers of elements in each block and the horizontal axis gives the diagnosis of the blocks. It is important to note that no goat elements are recorded, only those of the Soay sheep. In addition certain characters in the skull, atlas, axis, and pelvis were scored for male-like or female-like and the results are shown in the block diagrams of these elements.

A line drawing of each element is provided to show the points of measurement, signified by numbers, and the characters which are signified by capital letters. The same capital letters are used on the block diagrams and on the legends in which a short description is given of each character.

The mean lengths of the elements in the following descriptions are provided in order to give a general impression of the

Table 4 Length of outer curve (mm) of Soay horn sheaths

(a) Yearlings (1979)—Hirta data only

Sex	N	mean	range	st.dev	Coefficient of variation
male	33	184.4	123–224	25.6	13.9
female	11	70.4	17–109	33.9	48.2
castrate	4	99.5	78–111	–	–

(b) Three year old males—Hirta data only

Sex	N	mean	range	st.dev	Coefficient of variation
male	18	348	135–436	65.4	18.8
recalculated: excluding the one atypical stumpy horn (length 135)					
	17	360.4	261–436	39.4	10.9

Table 5 Soay sheep, horn inheritance. Phenotypes. Dams with single lambs.

		DAMS polled	 scurred/stunted horns	 fully horned
OFFSPRING (lamb):				
male	polled	–	–	–
	scurred/ stunted	–	–	–
	fully horned	7	1	6
female	polled	8	–	3
	scurred/ stunted	1	–	–
	fully horned	2	1	3
castrate	polled	6	–	–
	scurred/ stunted	1	–	–
	fully horned	1	–	4

Table 6 Soay sheep, horn inheritance. Phenotypes. Dams with twin lambs

DAMS	OFFSPRING (twin pairs)		
Horned	male horned female horned	female horned female horned	
Scurred/stunted	male horned castrate horned	female horned female horned	female horned female polled
Polled	male horned female polled	male horned castrate polled	
	castrate scurred female polled	male horned male scurred	

Table 7 Model of the genetic basis for the presence or absence of horns in the Soay sheep

Phenotype	Suggested genotype* [based on Ibsen (1944)]
horned male	ppHH hmhm srsr
horned female	ppHH HmHm srsr
hornless female	ppHH hmhm srsr or PPHH Hmhm srsr (Srsr)
scurred female	ppHH hmhm Srsr

Key to symbols
H horned gene (all sheep homozygous = HH) influenced by following 'factor pairs'
P = polled (epistatic to H)
p = absence of P
Hm = dominant to hm a modifier which causes an otherwise horned female to be hornless
Sr = gene for producing scurs (N.B. gene unable to express itself in the presence of P)

size of the bones. The 'combined mean lengths of the male and female elements' have been calculated from the measurement summaries of 'male aged', 'female aged', and 'male/female not aged' elements presented in the Appendix.

Skull

The skull of the sheep is made up of a great many distinct bones with joints that become completely fused in the adult animal, except for the lower jaw or mandible which always remains a separate movable element (described in the following section).

The skull of a horned and a hornless sheep are shown in the diagrams (Fig. 6 a–d) together with the points of measurement for the dimensions (1–13) which are recorded in the Appendix. The mean condylo-basal length for the sample of male Soay skulls (aged and unaged) is 198.06, for the female skulls (aged and unaged) it is 195.04, and for the castrates it is 220.42. Thus it can be seen that castration increases the length of the skull to a marked extent, a question which was discussed further in the section on castrates (p. 10).

Ageing of the skull can be carried out with considerable accuracy in the sheep and goat by examination of the state of eruption and wear of the cheek teeth (see p. 7).

The sex of the skull of the adult Soay sheep can be determined rather easily from the horn cores as described in the previous section (p. 10). The size of the horn cores has a direct relationship with the degree of robustness of the cranial region of the skull.

Because of the certainty with which the Soay skulls can be sexed the unaged, randomly-collected skulls were recorded as male or female when they were used in the scoring for sheep-like or goat-like characters and it is for this reason that all the skulls in the block diagrams (Fig. 7 A–J) are sexed.

As would be expected, considering the large number of separate elements that make up the skull, there are many characters which distinguish between sheep and goat. Ten of the characters described by Boessneck (1969) are discussed and figured here. The first three of these characters are on the facial region of the skull and the rest are on the cranial region.

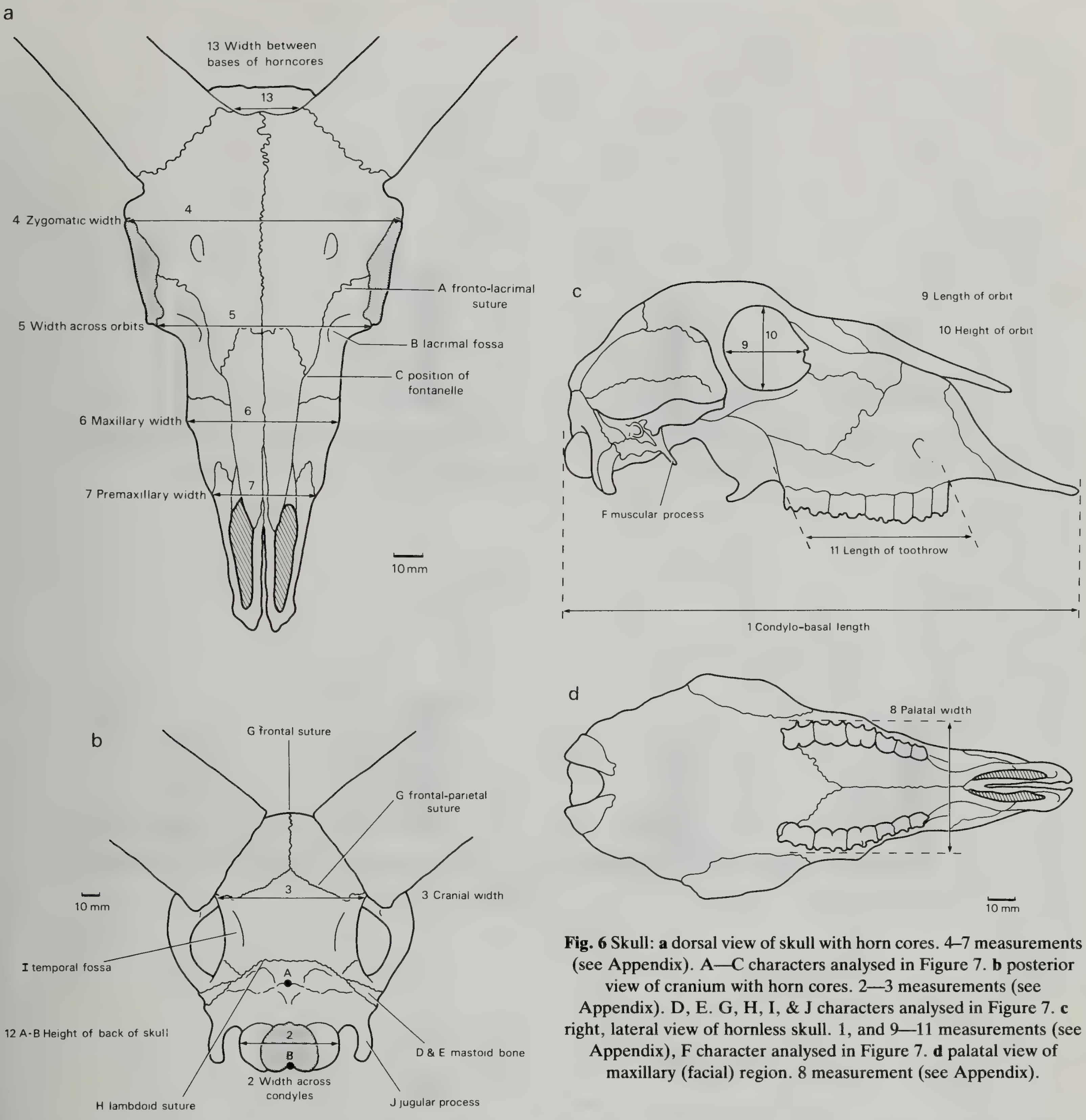

a
13 Width between bases of horncores
13
4 Zygomatic width
4
A fronto-lacrimal suture
5 Width across orbits
5
B lacrimal fossa
C position of fontanelle
6 Maxillary width
6
7 Premaxillary width
7
10 mm
c
9 Length of orbit
10 Height of orbit
9
10
F muscular process
11 Length of toothrow
1 Condylo-basal length
d
8 Palatal width
10 mm
b
G frontal suture
G frontal-parietal suture
3
3 Cranial width
10 mm
I temporal fossa
A
12 A-B Height of back of skull
2
B
D & E mastoid bone
2 Width across condyles
H lambdoid suture
J jugular process

Fig. 6 Skull: **a** dorsal view of skull with horn cores. 4–7 measurements (see Appendix). A—C characters analysed in Figure 7. **b** posterior view of cranium with horn cores. 2—3 measurements (see Appendix). D, E. G, H, I, & J characters analysed in Figure 7. **c** right, lateral view of hornless skull. 1, and 9—11 measurements (see Appendix), F character analysed in Figure 7. **d** palatal view of maxillary (facial) region. 8 measurement (see Appendix).

FACIAL REGION. The suture between the frontal and lacrimal bones (Fig. 6a A) is supposed to be nearly straight and with few serrations in sheep while it is indented and serrated in goats but, as shown in Figure 7 A, this is not a sound discriminant in the Soay skull. Character B (Figs 6a B, 7 B), the presence of a lacrimal fossa in sheep, is the best known distinction and can always be used for separating the facial region of the skull of a sheep from that of a goat. The fossa can be seen as a deep indentation in front of the orbit and it is never present in goat skulls. The third character is also a good discriminant although a male and two female skulls were scored as intermediate. This is the absence of a permanent fontanelle between the nasal and the lacrimal bone in the sheep (Figs 6a C, 7 C).

CRANIAL REGION. Characters D and E (Fig. 6b) are concerned with the mastoid process, the bone which lies between the squamous temporal bone and the paramastoid (jugular) process. In the sheep the mastoid is a small flat bone and not a process; it is wedge-shaped with no lateral projection as is found in the goat (character D) and it has a constriction or concave profile in its mid-line (character E). As can be seen from Figure 7 D and E there were some skulls that were scored as intermediate for these two characters but none was goat-like.

Character F (Fig. 6c) is to be seen on the very delicate muscular process of the tympanic bone which is long and pointed in sheep skulls but short and blunt in goat. Figure 7 F shows that this is a sound character, with few intermediate

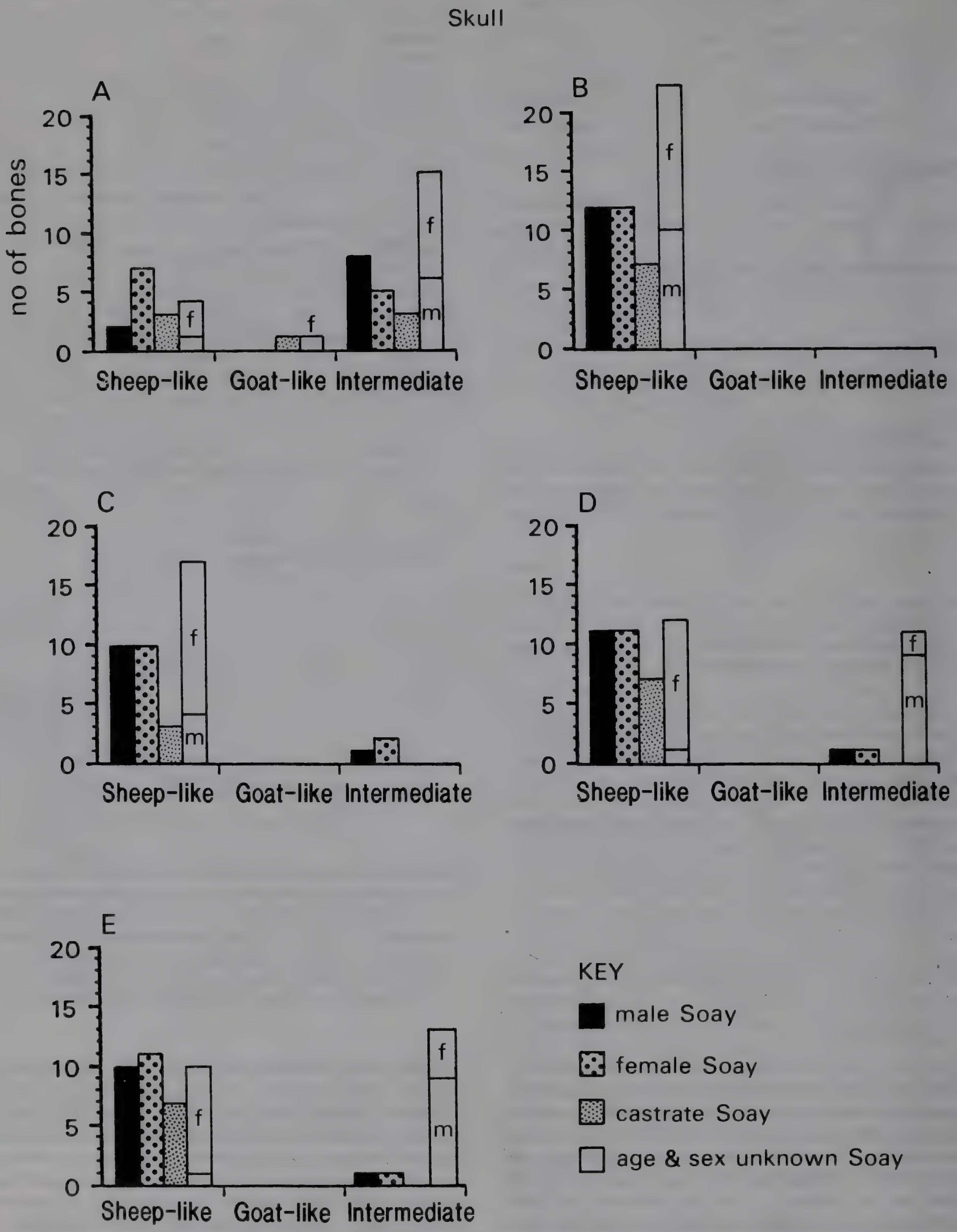
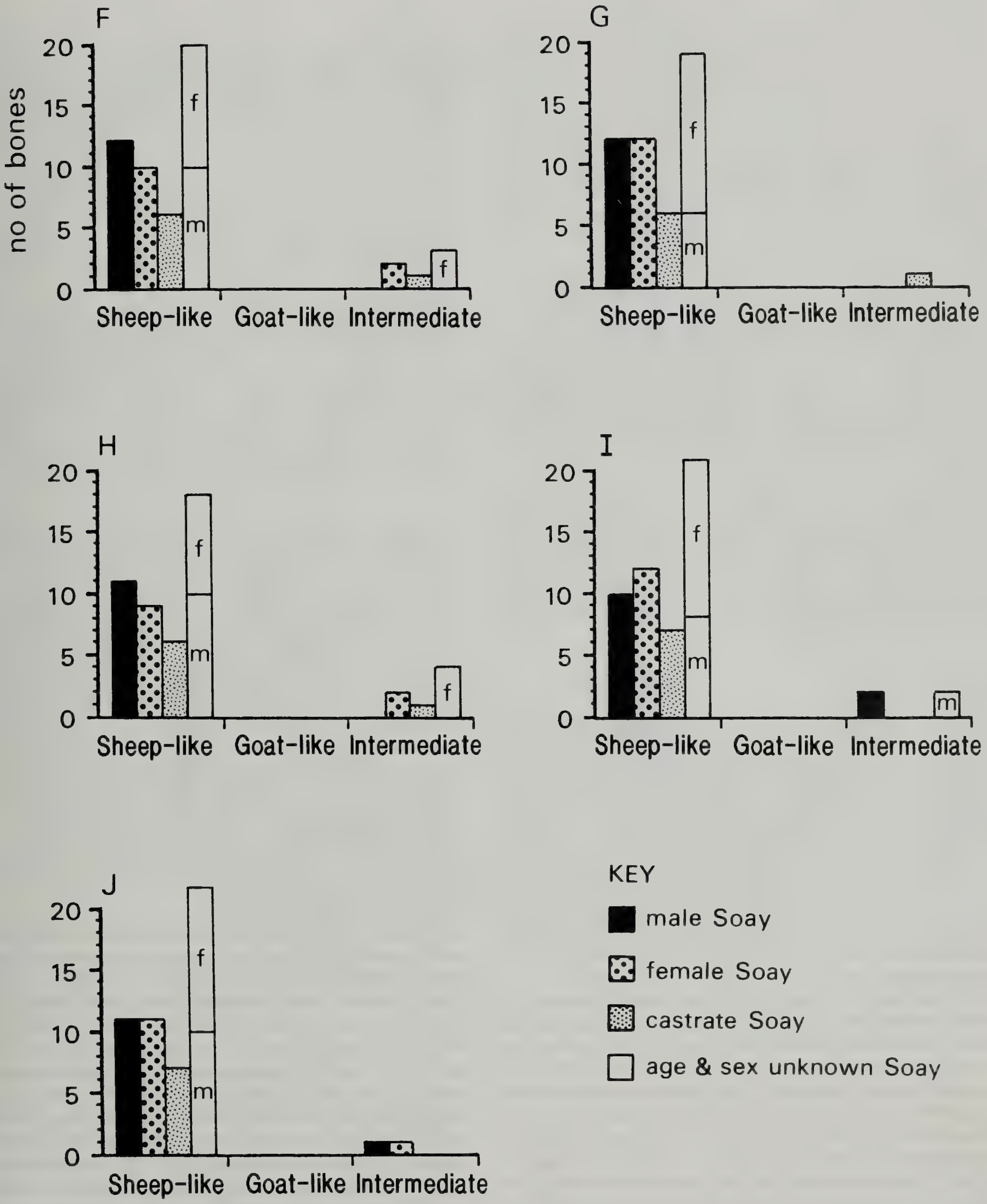


Fig. 7 Skull: analysis of sheep-like and goat-like characters. A fronto-lacrimal suture: sheep—straight with few serrations; goat—indented and serrated. B Lacrimal fossa: sheep—present, goat—absent. C fontanelle between nasal and lacrimal bone: sheep—absent, goat—present. D lateral projection of mastoid process: sheep—absent, goat—present. E shape of mastoid process: sheep—narrow and constricted; goat—broad. F muscular process of tympanic bone: sheep—long and pointed; goat—short and flat. G shape of frontal and fronto-parietal sutures: sheep—inverted Y-shape; goat—inverted T-shape. H shape of lambdoid suture: sheep—straight; goat—convex. I temporal fossae: sheep—wide apart; goat—closer together. J shape of paramastoid (jugular) process: sheep—long and slender; goat—short and broad.

Skull


F
G
H
I
J
no of bones
0
5
10
15
20
f
m
Sheep-like
Goat-like
Intermediate
KEY
male Soay
female Soay
castrate Soay
age & sex unknown Soay

specimens, but the process is most likely to be broken off in archaeological material.

The last four characters in the cranial region are well-known diagnostic features: Character G is the shape of the suture between the frontal bones and the parietal bone which is like an inverted Y in the sheep when looked at from the back of the skull, and like an inverted T in the goat (Figs 6b G, 7 G).

Character H is the shape of the lambdoid suture which separates the fused parietal and interparietal bones from the squamous part of the occipital bone (Fig. 6b H). In the sheep this is curved upwards and has a semi-circular or convex profile while in the goat it runs straight across the back of the skull. This is also a sound character in the Soay skulls although there are a few intermediate specimens (Fig. 7 H).

The ninth character (I) is seen in the shape of the temporal fossae which lie on either side of the fused parietal and interparietal bones. These fossae are wide apart in the sheep and close together in the goat (Figs 6b I, 7 I).

The proportional differences in the shape of the cranium in the sheep and goat can be expressed as ratios of measurements as described by Boessneck (1969) who called them the parietal index and the lambdoid index. These indices were calculated for the Soay skulls and they fell within the ranges published by Boessneck but the figures are not recorded here because visual inspection of the bones provides a definitive separation between sheep and goat, so that measurement is unnecessary.

The final character for distinction in the cranium is the shape of the paramastoid (jugular) process which is longer and thinner in sheep than in goats, so that it projects well below the level of the occipital condyles (Figs 6bJ, 7J). This can also be seen to be a sound character, although, as with the muscular process of the tympanic bone, it is seldom preserved in skull fragments from archaeological sites.

Mandible

The lower jaw, or mandible, consists of two elements, the left and right rami which are joined by a symphysis at the anterior, incisor-region. This symphysis hardly ever fuses completely in the sheep, except in very old animals. Each half of the mandible is divided by the angle into a horizontal ramus which holds the incisors and cheek teeth and a vertical ramus which articulates, by means of the condyle, with the zygomatic process of the squamous temporal bone. Anterior to the condyle and divided from it by a notch is the coronoid process which, in the articulated mandible, extends upwards into the temporal fossa and provides attachment for the temporal muscle (Fig. 8).

When separated from the skull it is not possible to establish the sex of the mandible of the Soay. The mean length of the combined male and female mandibles is 149.01, for the castrates it is 167.87, and for the goats it is 180.10 (see Appendix). As with the skulls it can be seen that the length in the castrates is much extended, the extra growth being in the facial region.

The mandible cannot be readily distinguished between sheep and goat and neither of the characters described in Boessneck *et al.* (1964) was found to be sound. The angle of the mandible is supposed to be more oblique in the sheep than it is in the goat but with one intermediate exception all the Soays had the acute angle that is described as goat-like (Figs 8 A, 9 A). The ventral margin of the horizontal ramus (Fig. 8 B) is described in the same work as more convex in the sheep but it can be seen from Figure 9 B that this character cannot be used, either, as a discriminant. In general it can be asserted that the mandible of the Soay is rather more shallow-boned and straight than is found in many breeds of sheep, perhaps because the teeth are relatively low-crowned.

Vertebrae

The usual number of vertebrae in the spinal column of the sheep is 7 cervical, 13 thoracic, 6 lumbar, 4 sacral, and 18 caudal. However, there may sometimes be 7 lumbar and the caudal vertebrae can vary between 3 and 24 depending on the breed. Only the atlas and axis, the first two of the seven cervical vertebrae found in all mammals, have been included in this study. Characters that discriminate between sheep and goat in the remaining cervical vertebrae, as well as in the thoracic and lumbar vertebrae have been described by Boessneck *et al.* (1964) and in the sacrum by Boessneck & Meyer-Lemppenau (1966).

There is normally a marked sexual dimorphism in the atlas and axis of caprines, those of males with large heavy horns being much more robust than those of females. When attempting to differentiate between these elements in the sheep and goat it is therefore necessary to first separate the males from the females. The works of Boessneck *et al.* (1964) and Boessneck (1969) provide characters for the testing of these discriminants on the atlas and axis of the Soay sheep.

ATLAS. The function of the first cervical vertebra, or atlas, is to support the head and to act as a pivot. It differs from all other vertebrae in lacking a spinous process and a body or centrum. The bone ossifies from four centres and is in three pieces at birth, the ventral arch and two lateral parts. These are usually fully fused in the sheep by 6 months of age.

In the sample of atlas vertebrae from the Soays the mean total length of the male elements is 49.74, for females it is 45.82, and for the castrates it is 50.10. The mean length for the small sample of combined male and female goats is 70.58.

As can be seen from the Appendix the majority of the bones of the castrates are markedly longer than those of the entire males. In contrast, the lengths of the atlas (and the axis) in the castrates are no longer than those of the entire males. Perhaps this is because the size of the vertebra is dependent on the size of the horns and in the castrated male growth of the horns is inhibited so that they only compare in size with those of female sheep.

According to the criteria of Boessneck (1969) the diagnostic parts of the atlas are the modified transverse processes on the posterior ends of the wings (Fig. 10a A, B). These should be short in the sheep and long in the goat. In female sheep the processes should be short and pointed, in male sheep short and blunted, in female goats long and blunted, and in male goats long and pointed. However visual assessment of the length and shape of the transverse processes failed to support any of these discriminants (Fig. 11 A, B) and neither did measurement of the ventral length of the bone against the total length (Fig. 10b). The ratio of these two lengths should give an indication of the relative length of the transverse processes, but there were not found to be any significant differences between the male and female elements, either in the sheep or goat or between the two genera.

A second character that was tested on the atlas vertebrae of the Soays was the shape of the ventral tuberosity (Fig. 10b C).

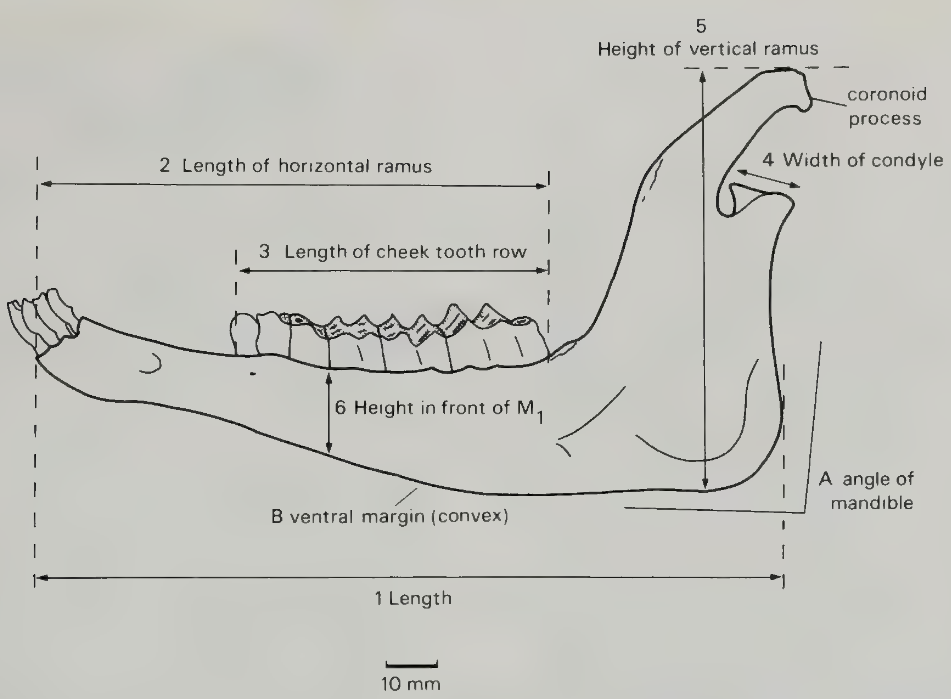

5
Height of vertical ramus
coronoid process
4 Width of condyle
2 Length of horizontal ramus
3 Length of cheek tooth row
6 Height in front of M_1
A angle of mandible
B ventral margin (convex)
1 Length
10 mm

Fig. 8 Mandible: lateral view of left ramus. 1—6 measurements (see Appendix). A, B characters analysed in Figure 9.

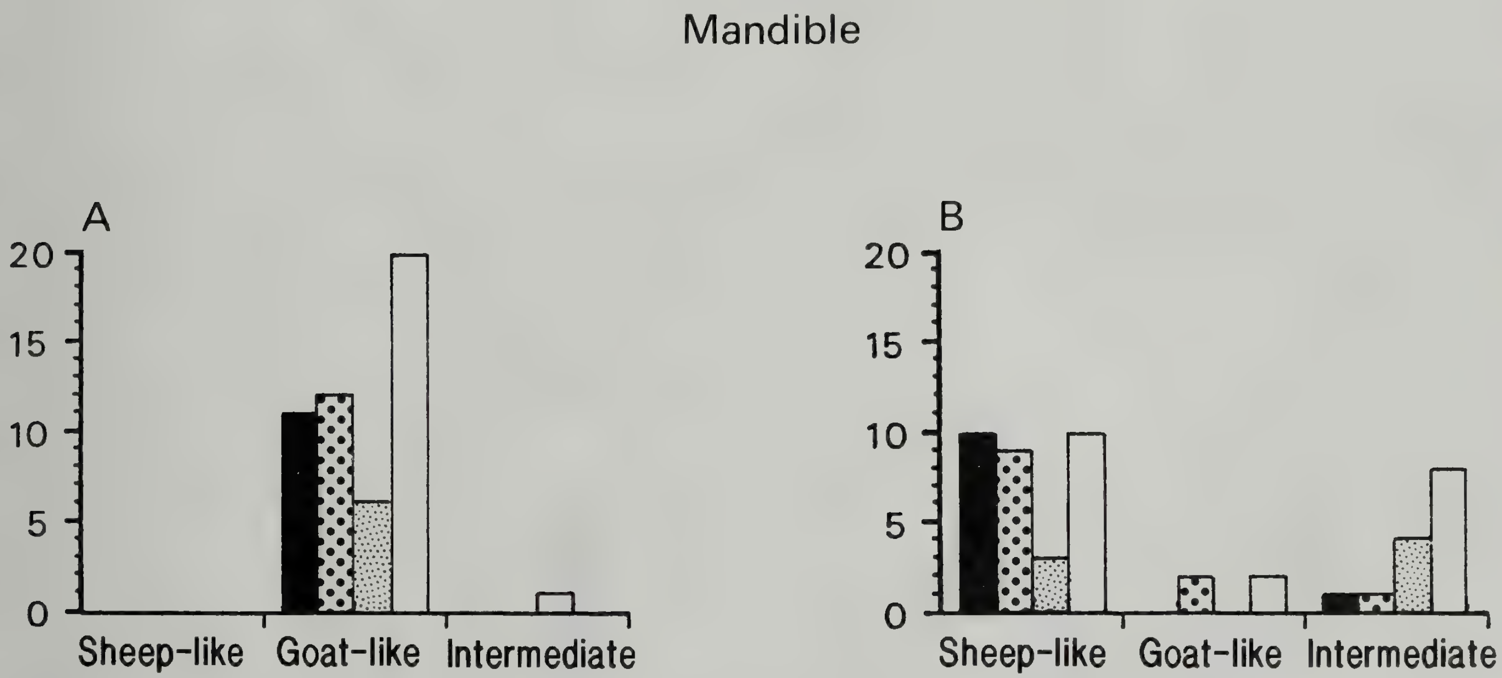


Fig. 9 Mandible: analysis of sheep-like and goat-like characters. A angle between horizontal and vertical ramus: sheep—obtuse; goat—acute. B ventral margin of horizontal ramus: sheep—convex; goat—straight.

This should be broad and ill-defined in the sheep, while in the goat it is narrower, and more ridge-like. As can be seen from Figure 11c, however, this character was not found to be a valid discriminant with the sample of Soay elements.

Axis. The axis is the longest of the vertebrae and it is characterized by the odontoid process or dens which projects from the anterior end and articulates with the posterior surface of the atlas, resting on the ventral arch. The odontoid process is usually regarded as the displaced body of the atlas and it ossifies from a centre separate from the rest of the axis. The centrum of the axis is usually fully fused by 6 months.

The mean length of the axis vertebrae in the sample of male Soays is 50.41 for the females it is 40.93, for the castrates 53.39, and for the male and female goats 69.87. As with the atlas vertebra it is notable that the mean length for the castrates is only slightly longer than for the male Soays, showing that this bone does not increase in length to the extent of other bones in the skeleton (Table 2; Appendix).

As described by Boessneck (1969; in which the bone is called the epistropheus) the spinous process of the axis is sexually dimorphic and it is shorter in sheep than it is in goats. The shape of the spinous process (Fig. 12b A, B, C) is dependent on the absence or presence of horns and their size. Assessment of the relative size and shape of the spinous process is shown in Figure 13 A–C. In the sheep the spinous process is short with a rounded or pointed cranial end and a broad rounded caudal end. In the goat the whole process is longer and the ends project further than they do in the sheep. Although, as can be seen from Figure 13 A, B, C, there are some intermediate elements, in general the axis vertebrae of the Soays conform to the sheep pattern. This is supported by measurement of the spinous process; the ratio of the length of the process relative to the length of the body including the

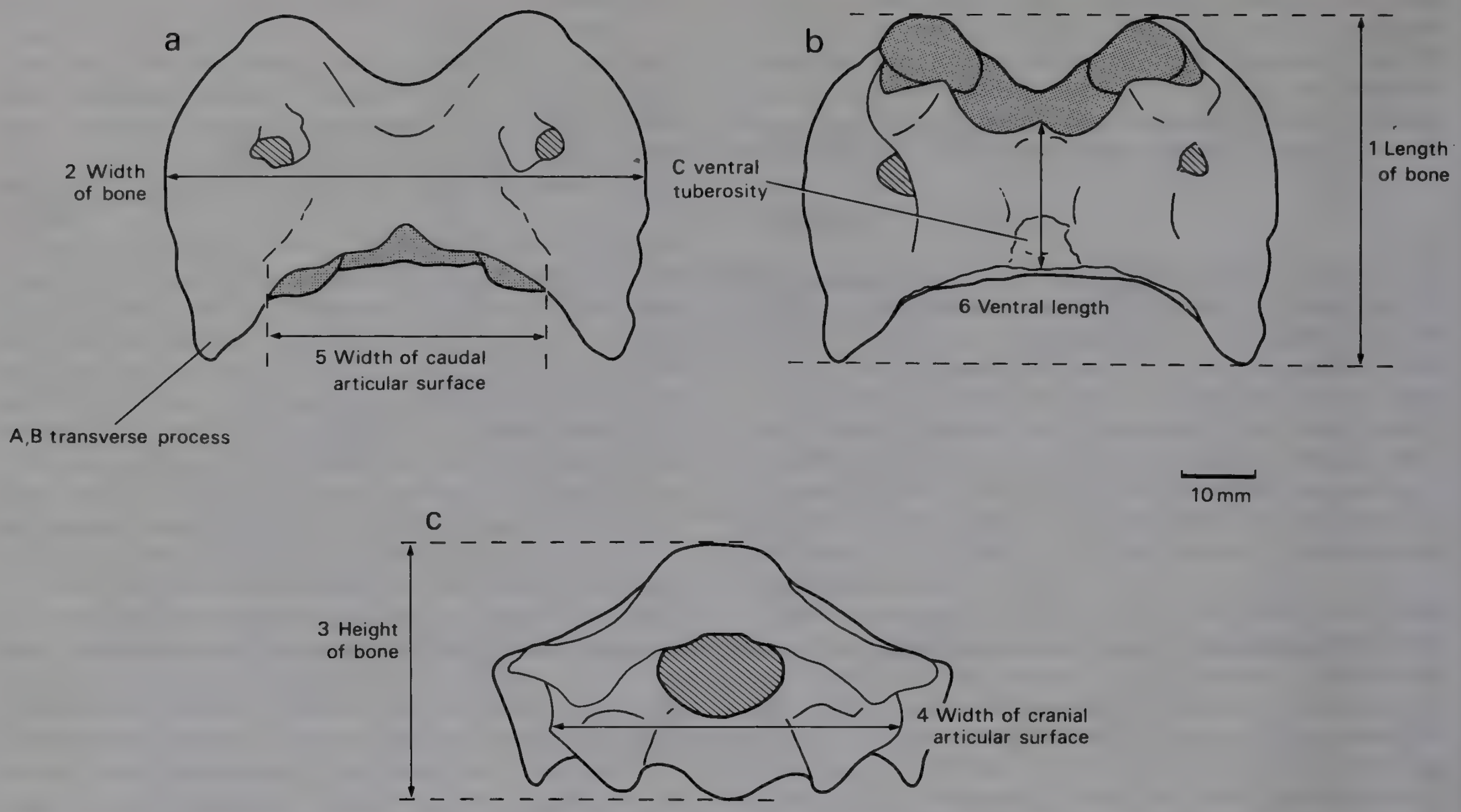

a
2 Width of bone
5 Width of caudal articular surface
A,B transverse process
b
C ventral tuberosity
6 Ventral length
1 Length of bone
10 mm
c
3 Height of bone
4 Width of cranial articular surface

Fig. 10 Atlas: **a** dorsal view. **b** ventral view. **c** cranial view. 1—6 measurements (see Appendix). A, B, C characters analysed in Figure 11.

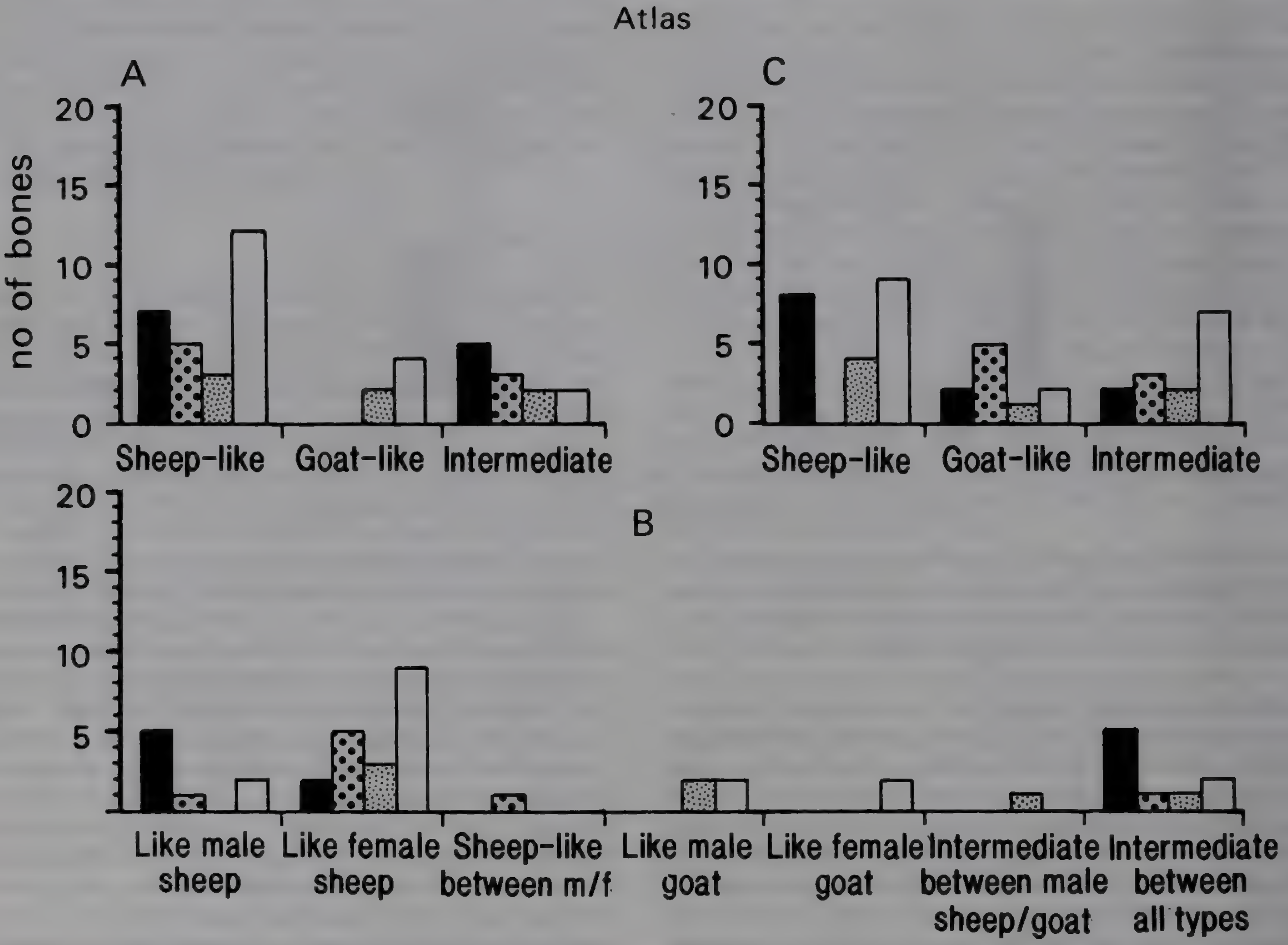


Fig. 11 Atlas: analysis of male-like & female-like and sheep-like & goat-like characters. A length of transverse process: sheep—short; goat—long. B shape of transverse process: sheep male—short and blunted; sheep female—short and pointed; goat male—long and pointed; goat female—long and blunted. C shape of ventral tuberosity: sheep—broad and ill-defined; goat—narrow and ridge-like.

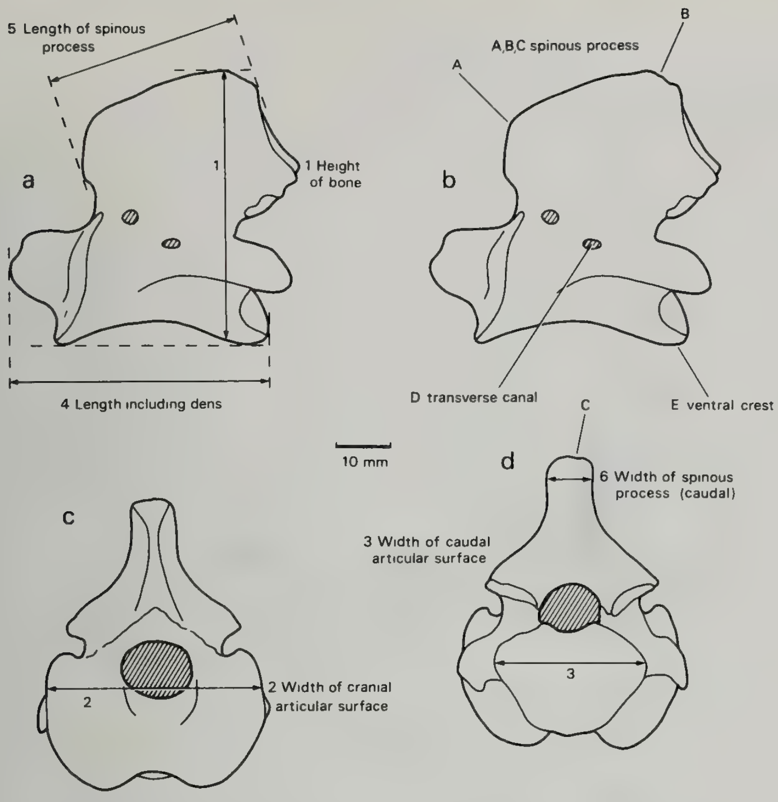

5 Length of spinous process
B
A,B,C spinous process
A
1
1 Height of bone
a
b
4 Length including dens
D transverse canal
C
E ventral crest
10 mm
d
6 Width of spinous process (caudal)
c
3 Width of caudal articular surface
3
2 Width of cranial articular surface
2

Fig. 12 Axis: **a** and **b** lateral views. **c** cranial view. **d** caudal view. 1–6 measurements (see Appendix). A—E characters analysed in Figure 13.

odontoid process has a maximum of 84% for the Soays and a minimum of 89% for the goat. However the ratio of width of the caudal end to length of the spinous process does not show a significant difference between the Soays and goats for this character, thus agreeing with the assessment in Figure 13C, in which there is a high proportion of intermediates.

Figure 13 D shows that the transverse canal (Fig. 12b D) is present in all the axis vertebrae of the Soays, this being a sheep-like character often absent in the goat.

The development of the ventral crest was used by Boessneck (1969) as a determinant of sex and genus (Fig. 12b E) In old male sheep the ventral crest broadens and flattens at the caudal end while in the male goat it forms a more angular dome. The axis vertebrae of the male Soays conform well to this discriminant as shown in Figure 13 E.

Scapula

The scapula or shoulder blade occupies a movable position on the anterior part of the thorax. In sheep as in all ungulates which have no clavicle the bone is attached to the axial skeleton only by muscles. The scapula is a flat bone with a spine that runs longitudinally along the lateral side for the attachment of the shoulder muscles. The two sides of the spine are slightly hollowed and are known as the supra-spinous and the infra-spinous fossae. The medial side of the bone has no spine and is known as the subscapular fossa.

The shallow cup-shaped distal end of the scapula, known as the glenoid cavity, articulates with the head of the humerus (Fig. 14b). The glenoid cavity is not an epiphysis and ossifies before birth but its anterior margin is bounded by the coracoid process which (according to Silver (1969) where it is called the bicipital tuberosity) fuses in the sheep between six and eight months. In the collection of Soay sheep scapulae the coracoid process was only unfused in the foetal and newborn scapulae.

The mean height of the combined male and female scapulae is 134.65, that for the castrates is 151.07, and for the goat scapulae it is 177.40.

It is generally agreed that a sound character for distinguishing the scapula of the sheep from the goat is the convex 'bulge' or pecten that develops on the posterior (glenoid) border of the neck in sheep (Fig. 15a B). However it can be seen from Figure 16 B that four scapulae of Soays, two castrates and two males/females were scored as intermediate between sheep and goat for this character. This means that these scapulae had only a slight pecten.

From Figures 15b A, 16 A the concave profile of the anterior (coracoid) margin of the scapula is a good character for distinction with no intermediates. The concavity is dependent on the relative length of the proximal end of the blade which is greater in the sheep than in the goat. The shape of the subscapular fossa (Figs 15b E, 16 E) is also dependent on the width of the blade and shows considerable variation.

In the sheep the spinal tuberosity is according to Boessneck (1969) thick and curved in the sheep but in the Soay scapulae there are a certain number of intermediates for this character (Figs 15a C, 16 C). The angle of the spine as it projects from the blade of the scapula is generally more obtuse on the posterior side, that is it leans further over towards the anterior margin of the scapula, in sheep than in goats. As can be seen from the scores (Figs 15a D, 16 D) there are also a number of intermediates for this character.

Taking all the characters into consideration it is found that the scapula of the Soay, like many other elements, is more goat-like than is usual for the skeletons of improved breeds of sheep.

Humerus

In the living sheep, as in all ruminants, the humerus extends obliquely downwards and backwards. It articulates at its proximal end, in the shoulder joint, with the scapula, and at its distal end, in the elbow joint, with the radius and ulna.

The mean length of the combined male and female humeri is 131.31, that for the castrates is 141.86, and for the goat humeri it is 190.5. The 10 mm difference in length for the mean of the castrates over that for the entire males is notable and is discussed further under the section on castrates (see p. 9, Table 2). The distal end of the humerus is fused in the one year old sheep while the proximal end is still in the process of fusion in the three year old sheep (Fig. 2) which agrees with the data of Silver (1969).

The humerus of the Soay can be distinguished from that of the goat rather easily. In the proximal end the best distinction is the angle of the lateral tuberosity which is broad and projects less far over the sulcus than in the goat where it is high and more pointed (Figs 17a A, 18 A) Below the lateral tuberosity there is the deltoid tuberosity which in the Soay humerus forms a sharp edge that is turned over while in the goat it is more rounded and less marked (Figs 17a B, 18 B). Another distinction was described by Boessneck (1969) in the position of the nutrient foramen on the shaft; this is usually on the posterior side in the sheep and on the lateral side in the goat (Figs 17b C, 18 C). In the distal end of the humerus there are four distinctions; in the sheep there is a thickening, causing a slight protruberance on the lateral border of the trochlear surface which is not present in the goat (Figs 17c D,

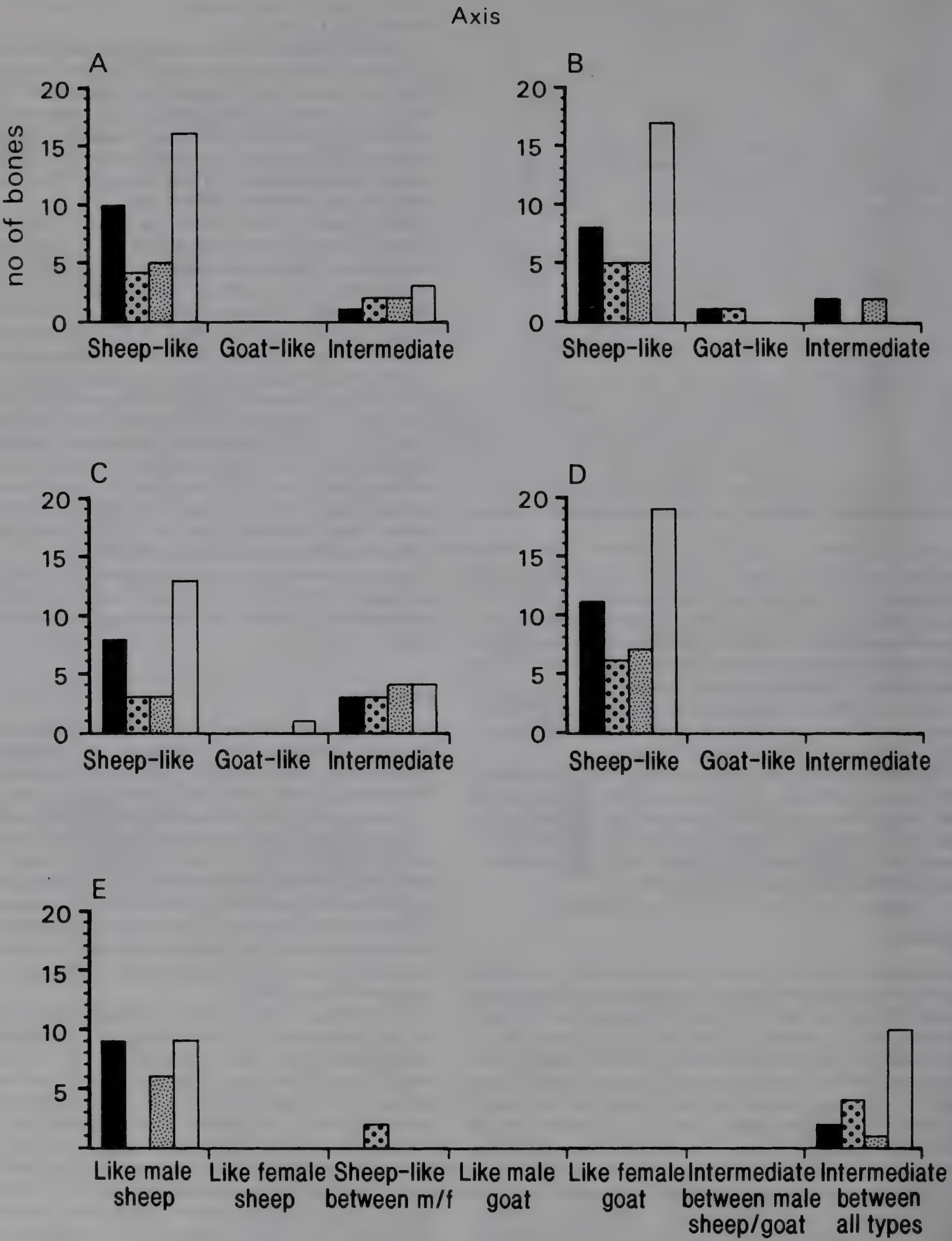


Fig. 13 Axis: analysis of male-like & female-like and sheep-like & goat-like characters. A shape of cranial end of spinous process: sheep—short and rounded or pointed; goat—long and projecting. B shape of caudal end of spinous process: sheep—rounded; goat—angular. C shape of crest of spinous process at caudal end: sheep—rounded; goat—angular. D transverse canal present in sheep; absent in goat. E shape of ventral crest at caudal end: sheep male—broad and blunt dome; goat male—a more angular dome.

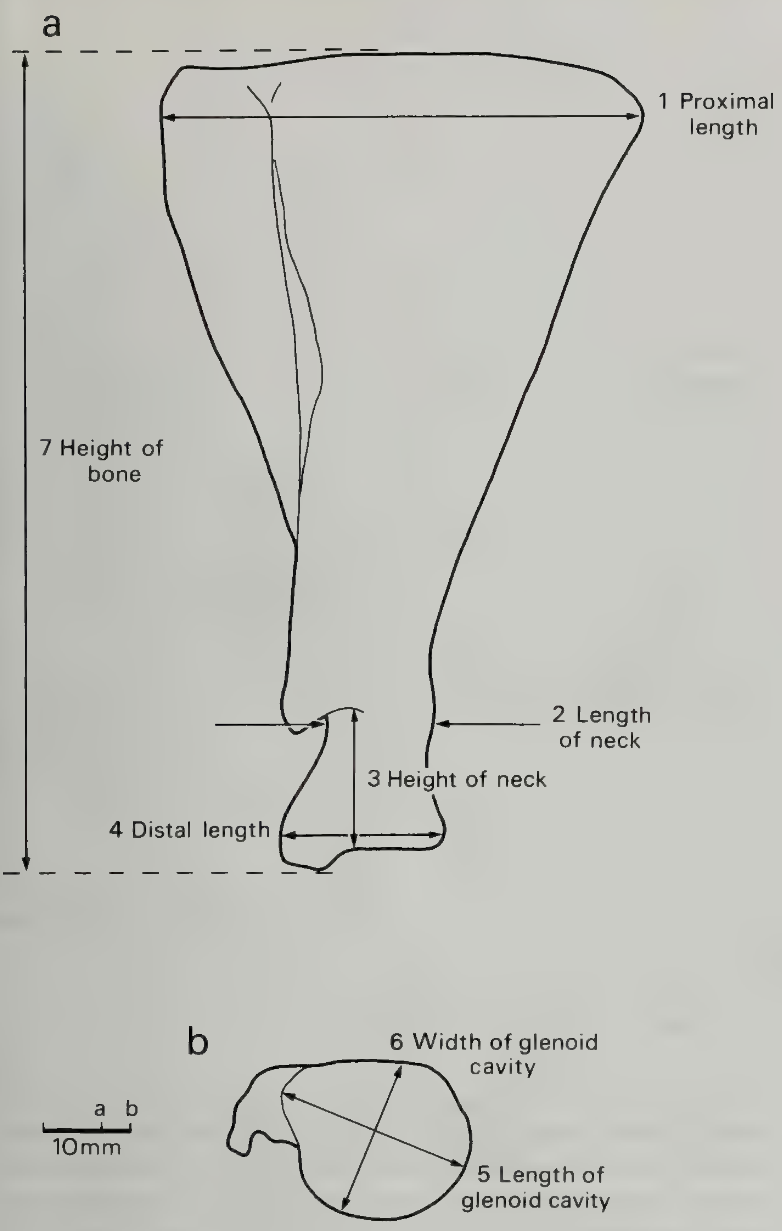


Fig. 14 Left scapula. **a** lateral view. **b** ventral view of glenoid cavity. 1–7 measurements (see Appendix).

18 D); the pit in the lateral epicondyle is surrounded by a marked ridge or crest in the sheep which is not present in the goat (Figs 17c E, 18 E); and the shape of the medial epicondyle is different in the sheep and goat, being rounded and having either a right- or an obtuse-angle in the sheep and being 'cut off obliquely' in the goat (Figs 17c F, 18 F). The fourth distinction is determined by measurement of the distal condyle which is higher in the sheep than in the goat, so that the ratio of height of condyle to distal width of bone is usually more than 46% in the sheep and less than 46% in the goat.

The least consistent of all these characters for distinction of the humerus, in the Soay, is the thickening of the lateral border of the distal trochlear surface (Fig. 17c D). Figure 18 D shows that six of the humeri are scored as goat for this character and eight are intermediate between sheep and goat.

Radius and ulna

These two bones form the part of the forelimb below the elbow joint. Muscles attached to the olecranon process of the ulna and the humerus enable the joint to move in flexion and extension with the action of a hinge. The radius is a larger bone than the ulna and the two shafts may be fused in the inter-osseous space at their proximal ends. The distal end of the radius articulates with the carpal bones which form the first section of the manus. In ungulates this joint is commonly known as the 'knee'. The carpal bones have not been included in this analysis of the skeletal elements of the Soay.

The mean length of the combined male and female radii is 139.05, for the castrates it is 153.83, and for the goats it is 185.40. The length of the ulna was not measured because of its curved profile; however, the mean length of the olecranon process in the combined male and female sample is 36.72, in the castrates, 41.64, and in the goats, 52.64.

Silver (1969) gives an age of 6–8 months for the fusion of the proximal epiphysis of the radius. In the Soay radii the proximal epiphysis is unfused in the newborn lambs and fully fused in the one year olds. As can be seen from Figure 2 the distal epiphysis of the female radius of the three year olds is fused while in the nine male, three year old radii the distal epiphyses are unfused in seven, beginning to fuse in one, and part fused in one. There are eight male ulnae, two with unfused olecranon processes, four part fused and three fused. These fusion times for the distal end of the radius and the olecranon of the ulna are later than those recorded by Silver (1969) which are three years for the distal radius and two and a half years for the olecranon.

The most distinctive feature of the sheep radius is the formation of a 'ledge' on the lateral border of the proximal epiphysis which is not found in goats (Figs 19b B, 21 B). An easy distinction is generally assumed to be the lack of fusion between the proximal articular surfaces of the radius and ulna, but in the Soay specimens a number are fused or part fused (Figs 20a A, 21 A). Distinctions in the distal end of the radius are difficult to describe; however, a long narrow facet (the radiale facet of Boessneck, 1969) for articulation with the scaphoid seems to be typical of the sheep (Figs 19c C, 21 C).

The ulna i not very easy to differentiate between sheep and goat. According to Boessneck (1969) the medial edge of the olecranon process should be slightly convex in sheep while in the goat it is almost straight, but the scores for this character in the Soays show a high proportion of intermediates (Figs 20b D, 21 D).

Measurement of the olecranon provides two indices that can discriminate sheep from goat. The olecranon process is usually longer in goats so that if the length is divided by the depth (Fig. 20a) an index of less than 160% will indicate that the bone is sheep, while the proximal end of the bone is thicker in goats so that if the index of width divided by depth is less than 46% (Fig. 20c) then again the bone is probably sheep, but for both characters a higher index cannot be taken as definitive of goat as some of the Soay ulnae have long and thick olecranons.

Pelvis

Apart from the skull the pelvis is the most complicated bone in the skeleton. It links the vertebral column and tail with the hind limbs and, in the female, it provides a channel through which the foetus is born. Like the scapula the pelvis is generally regarded as part of the appendicular skeleton. It is joined to the axial skeleton at the sacrum by the sacro-iliac joint, which has only a very limited degree of movement, its stability being secured by the very powerful sacro-iliac ligaments.

In the adult sheep, as in all mammals, the pelvis, or pelvic girdle, consists of two bones known as the left and right

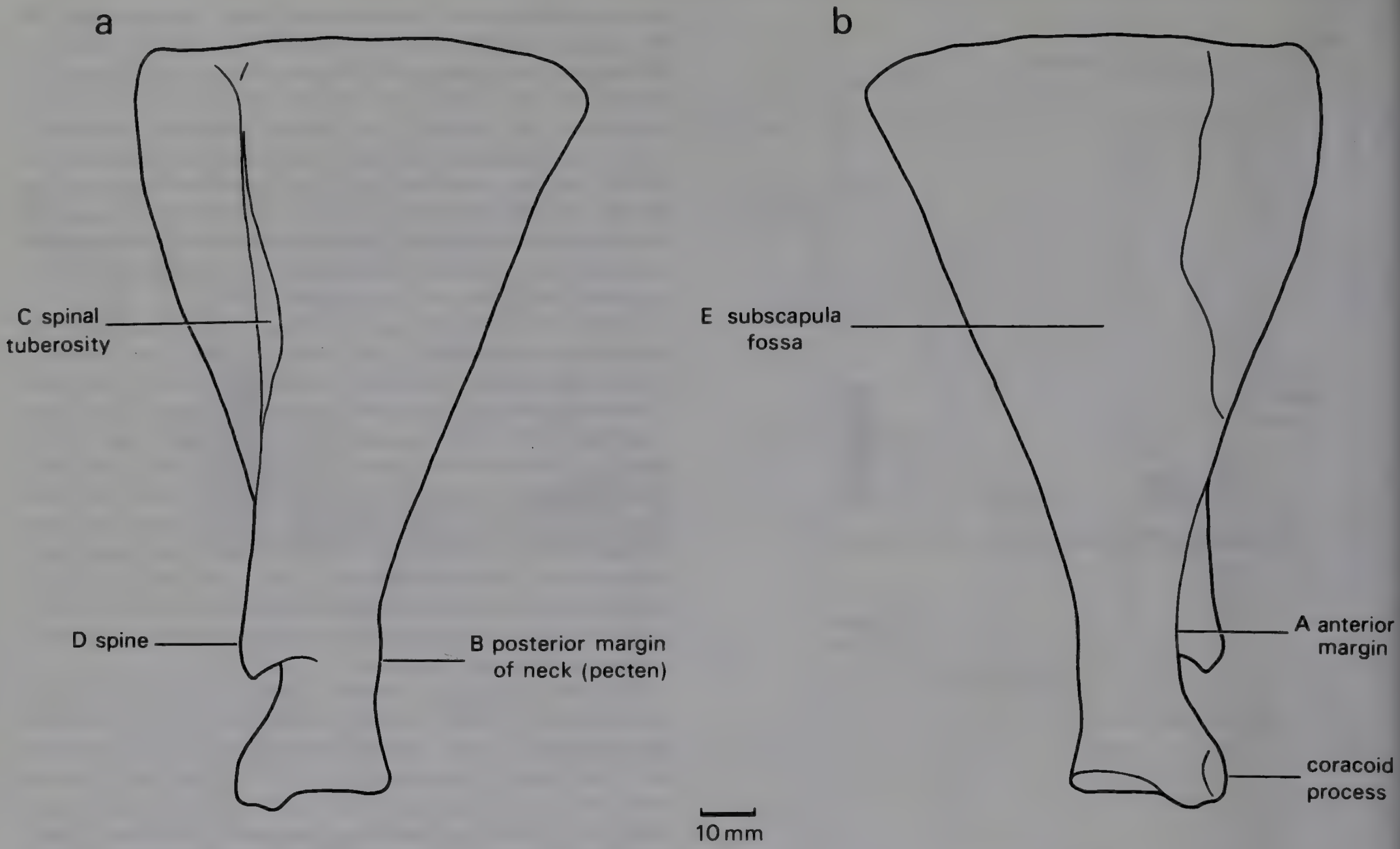


Fig. 15 Left scapula: **a** lateral view. **b** medial view. A–E characters analysed in Figure 16.

innominate bones or *os coxae*. These two bones are joined ventrally in the mid-line of the body at the pubic symphysis. In the foetus and in young mammals each innominate bone consists of three separate elements, the ilium, ischium, and pubis which fuse as the animal grows until the symphyses are completely invisible to the naked eye. In the sheep this usually occurs by the age of three and a half years (Silver, 1969). However, because of its complicated structure the pelvis is not a very useful bone for the assessment of age and it has not been included in Figure 2.

In the sample of pelvic bones of the Soays the mean total length of the male innominate bones is 185.69, for the females it is 175.95, and for the castrates 184.5. The mean width of the pelvis across the acetabula is 95.02 in the males, 93.87 in the females, and 97.75 in the castrates (Fig. 22; Appendix). These figures are of interest in showing that in overall dimensions the female pelvis is wider for its length than that of the male and the castrate; greater width being required in the female for the passage of the foetus at birth.

Boessneck (1969) claimed that the ilium in sheep and goats is longer in the female than in the male but measurement of this element in the Soays does not support this (Fig. 22; Appendix). However, three qualitative characters described by Boessneck as being sexually dimorphic do discriminate satisfactorily between the male and female Soay innominates. The first character is the shape of the iliac wing (Fig. 23 A) which is blunt and usually rounded in male sheep and goats, while it is extended and pointed in female sheep and goats. The second character is to be seen in the pubic bone (Fig. 23 B): in male sheep and goats the pecten which forms on the robust ventral border of the bone is rounded and indistinct, while in female sheep and goats this border is slender and the pecten forms a sharp ridge. The third character is seen in the shape of the ilio-pectineal eminence (Fig. 23 C). This is pad-shaped in male sheep and goats while it is sharp-edged, or even developed as a point, in females. The block diagrams shown in Figure 24 A, B, C show that these characters do separate male and female innominate bones although there are a few intermediate specimens. The innominate bones of the castrates, on the other hand, are anomolous and fall into all three categories of male, female, or intermediate.

It is not very easy to distinguish between the innominate bones of sheep and goats but there is one feature on which they can be separated. In goats the anterior end of the obturator foramen is extended forwards into a small semi-circular notch which leads into the dorsal side of the acetabulum (Fig. 23 D). This obturator notch is not present on the innominate bones of the Soays although it appears to be very slightly developed in one element and so was scored as intermediate (Fig. 24 D).

A second, generic character that can be used to separate female sheep from goats is the development of a muscle ridge on the ventral surface of the body of the ileum (Fig. 23 E) but this is not present in male sheep or goats. In female sheep the ridge is short and narrow, giving a distinct demarcation to the pit for the rectus femoris muscle, while in female goats this area is longer and more strongly ridged. Figure 24 E shows that there is a good separation for this character in the female innominates which all fall into the 'female sheep-like' character. The male innominates also conformed in having no muscle ridge but five of the seven castrates had developed a ridge as in the females.

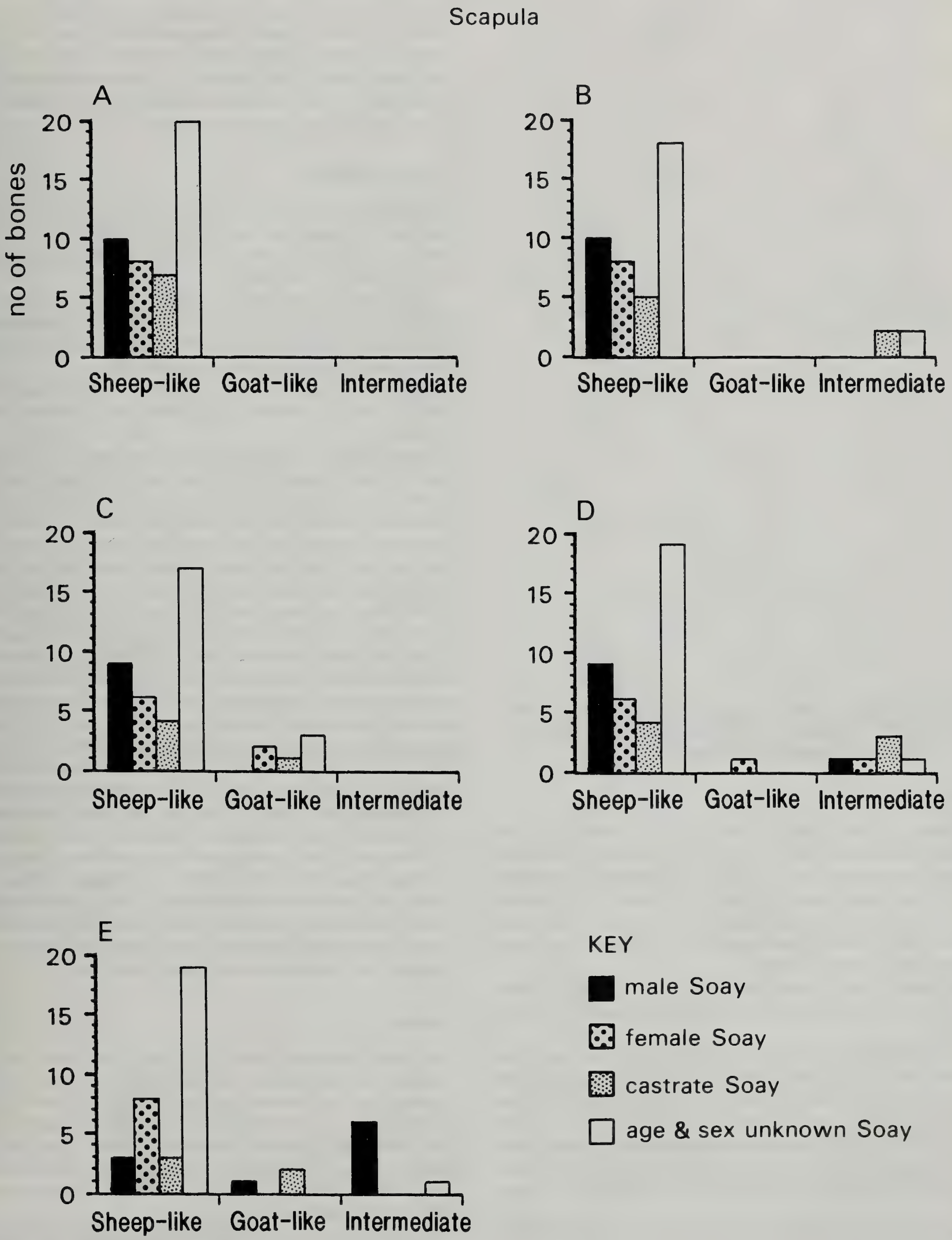


Fig. 16 Scapula: analysis of sheep-like & goat-like characters. A shape of anterior margin: sheep—strongly concave; goat—less concave. B pecten on posterior margin: sheep—present; goat—absent. C shape of spinal tuberosity: sheep—thick and curved; goat—sharp and runs in a straight line. D angle of spine: sheep—obtuse: goat—acute. E shape of subscapular fossa: sheep—broad and flat: goat—narrow and restricted by a distinct eminence towards the cervical border.

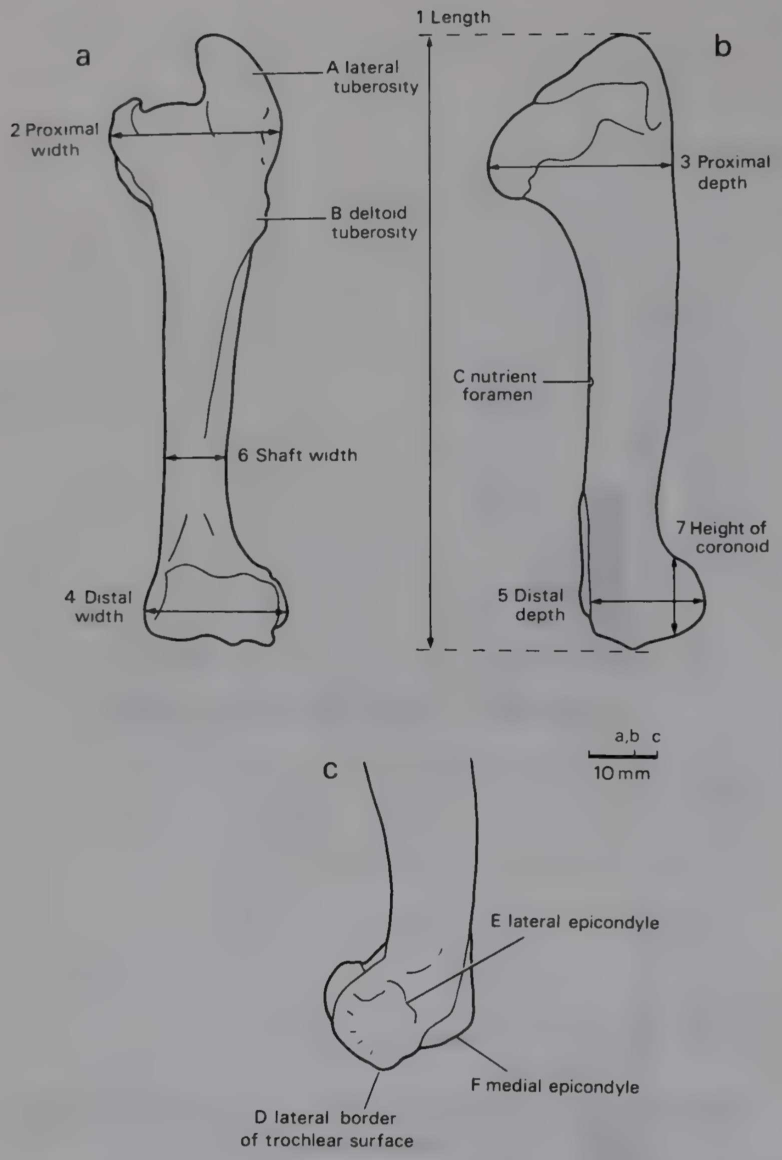


Fig. 17 Left humerus: **a** anterior view. **b** medial view. **c** lateral view of distal end. 1–7 measurements (see Appendix). A–F characters analysed in Figure 18.

Femur

The femur is an equivalant bone to the humerus of the forelimb; it connects the hip joint at its proximal end with the stifle joint at its distal end. The stifle joint, which is equivalent to the human knee, unites the end of the femur, the proximal end of the tibia, and the patella. The femur is the most massive bone in the skeleton and it stretches downwards and forwards in the living animal.

The mean length of the the combined male and female femora is 161.34, for the castrates it is 174.65 and for goats it is 202.70.

Silver (1969) gives 2½–3 years for the age of fusion of the proximal end of the femur (head and greater trochanter) and 3–3½ years for the distal epiphysis. In the femora of the Soay sheep (Fig. 2) only one proximal and one distal end are fused from the three year old male sheep, while the female femur has the proximal end fused and the distal end part fused which agrees with Silver's later date for the fusion of the distal end.

The proximal end of the Soay femur is relatively easy to distinguish from that of the goat as shown by the results of the character analysis given in Figure 27 A–C. In the sheep the head forms a continuum with the 'saddle' at the proximal end; in the goat the head is shaped like a ball and is cut off from the saddle (Fig. 25b A). The greater trochanter at the lateral side of the bone forms a separate epiphysis from the head and is flat across its top in the sheep, but this is a slightly less reliable character with some bones showing an intermediate state (Fig. 25d B). The square edge to this trochanter is also a character that is a nearly foolproof distinction (Fig. 25d C). There is only one distinguishing character at the distal end of the femur which is the absence of a synovial pit in the sheep (Figs 25b D, 27 D). However the frequency of absence of this pit in the goat has not been assessed.

Tibia and fibula

These bones are the equivalents of the radius and ulna of the forelimb although in the sheep, the fibula is extremely reduced. The tibia connects the stifle, a hinge joint like the elbow, with the hock joint.

In the sheep and goat the fibula is represented by a small projection on the lateral side of the proximal epiphysis of the tibia and by the lateral malleolus which articulates with the distal end of the tibia; there is no fibula shaft.

The mean length of the combined male and female tibiae is 188.55, for the castrates it is 209.63, and for the goat it is 246.30.

According to Silver (1969) the proximal end of the tibia should fuse between 3–3½ years and the distal end rather earlier at 1½–2 years. In the Soays the fusion times appear to be rather behind this, as shown in Figure 2. None of the proximal ends is fused at 3 years and one of the distal ends is still only part fused at 3 years. On the other hand the castrate has proximal and distal ends fused at 3 years 4 months.

The tibia is a bone that is difficult to distinguish between sheep and goat. The proximal end relies on the conformation of the nutrient foramina. In the goat there is usually one circular foramen encircled by a wider pit. In the sheep there is no pit and there can be either one or several foramina that are placed flat on the surface of the bone (Fig. 26b A). The shape and position of these foramina are quantified in Figure 27 A, and it can be seen that there are only two elements in which the foramina do not conform to the typical arrangement.

Following Boessneck (1969) no characters were analysed for the distal end of the tibia. This has been done, however, by Prummel (1986) who gives a description of three distinguishing characters. One of these, the trapezoid shape of the distal end, can be seen in Figure 26c. In the goat this profile is nearly rectangular. In general the distal end of the tibia is rather variable in shape and is not considered to be a useful element for the distinction of sheep from goat.

Patella

This is a sesamoid bone that articulates with the distal trochlea of the femur; its function is to give increased leverage to the femoral muscles in the stifle joint. It is of interest that even this bone becomes rather longer in a sheep that has been castrated than in an entire ram. The mean length of the combined male and female patellae is 26.98, while for the castrate it is 28.12, and for the goat it is 37.53 (Fig. 28a, b; Appendix).

The bone has no epiphyses and so it cannot be aged. The patella was not included in the sheep and goat distinctions described by Boessneck (1969) but it was mentioned in the earlier work of Boessneck *et al.* (1964). On the antero-proximal face of the bone there is usually a sulcus

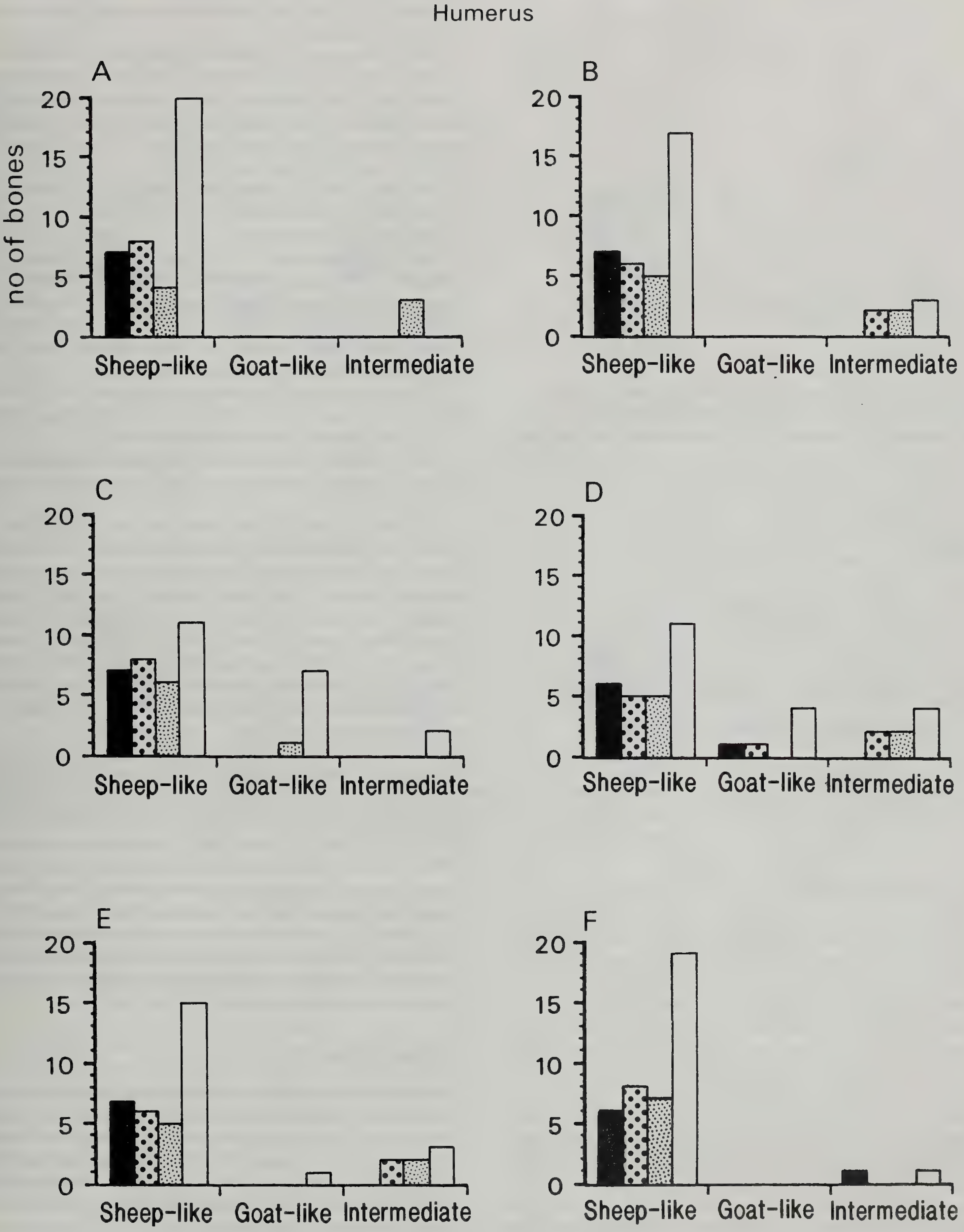


Fig. 18 Humerus: analysis of sheep-like & goat-like characters. A shape of lateral tuberosity of proximal articular surface: sheep—broad and low; goat—high and narrow. B shape of ridge below deltoid tuberosity: sheep—sharp and turned over; goat—straight and blunt, becoming indistinct distally. C position of nutrient foramen: sheep—on posterior side of shaft; goat—towards lateral side of shaft. D shape of distal trochlear surface: sheep—thickening on lateral side; goat—absent or slight. E shape of lateral epicondyle (distal end): sheep—crest on edge around pit; goat—crest absent. F shape of medial epicondyle: sheep—ends in an angle between acute and obtuse; goat—angle is cut off obliquely.

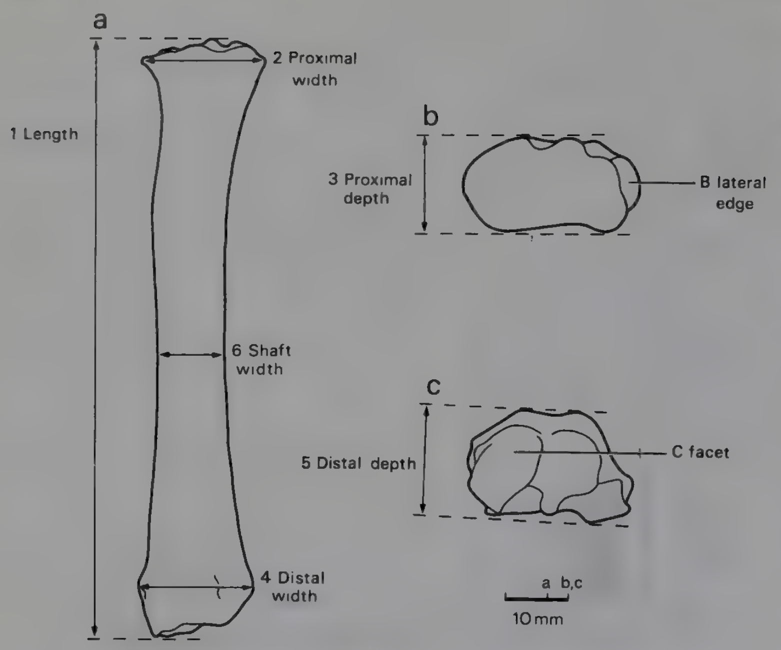


Fig. 19 Left radius: **a** anterior view. **b** dorsal view of proximal articular surface. **c** ventral view of distal articular surface. 1–6 measurements (see Appendix). B, C characters analysed in Figure 21.

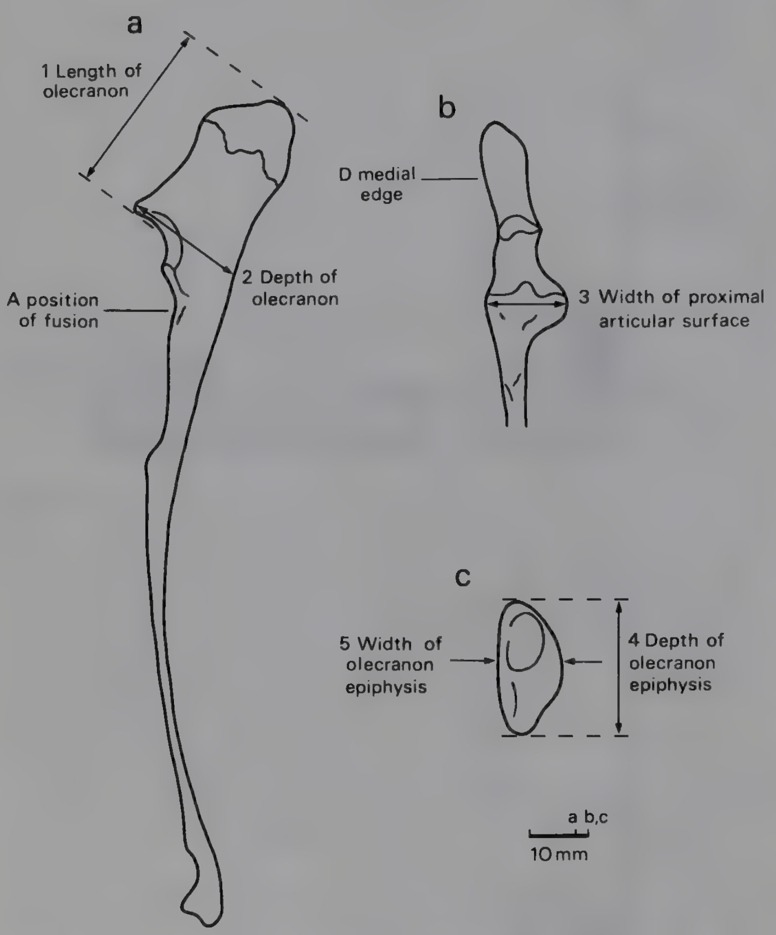

a
1 Length of olecranon
b
D medial edge
2 Depth of olecranon
A position of fusion
3 Width of proximal articular surface
c
5 Width of olecranon epiphysis
4 Depth of olecranon epiphysis
a b,c
10mm

Fig. 20 Left ulna: **a** lateral view. **b** anterior view. **c** dorsal view on olecranon process. 1–5 measurements (see Appendix). A, D characters analysed in Figure 21.

which is not present in the patella of the goat (Figs 28a A, 29 A).

Talus and calcaneum

Five bones make up the tarsus in the sheep, as in all Bovidae. These are the talus (often called the astragalus), the calcaneum, the scapho-cuboid, the large cuneiform, and the small cuneiform. Only the talus and calcaneum have been included in this study. The talus acts as a pulley and articulates with the distal end of the tibia and the scapho-cuboid as part of the hock joint.

The talus has no epiphysis but is nearly ossified before birth although there is some growth in the bone during the first year of life. The calcaneum has an epiphysis at the end of the tuber calcanei which according to Silver (1969) fuses in the sheep between 2½–3 years. It is fused in 3 out of the 6 three-year old male Soay calcanei (Fig. 2).

The mean length of the combined male and female tali is 25.21, that of the castrates is 26.63, and for the goats it is 32.66 (Fig. 28c; Appendix).

The best character for distinguishing the talus of sheep from goat is the distal end of the medial articular ridge which is weakly developed without a sharp angle in the sheep (Fig. 28d A). In the goat this ridge, in medial view, looks like a sharp point. One female and four castrate Soay tali are intermediate for this character (Fig. 29 A).

The calcaneum articulates with the posterior side of the talus and completes the pulley action of the hock joint, the whole being bound together with ligaments.

The mean length of the combined male and female calcanei is 50.62, for the castrates it is 54.57, and for the goats it is 66.27.

According to Boessneck (1969) the calcaneum of the sheep should be relatively easy to distinguish from that of goat. There are three characters that can be used. In the sheep the anterior border of the tuber calcanei is straight while it is slightly convex in the goat (Fig. 28g A) and the articular facets, which attach to the posterior side of the talus, are separate in the sheep and joined into one surface in the goat (Fig. 28f B). Both these characters are fairly consistent for the Soay calcanei but there are some intermediate bones (Fig. 29 A & B).

The third method of distinction lies in the proportion of the length of the lateral process of the calcaneum to the length of the condyle which articulates with the anterior lateral side of the talus (Fig. 28e 3:4). According to Boessneck (1969) this index should be more than 100% for the sheep and less than 100% for the goat, that is the lateral condyle is as long or longer than the lateral process in the sheep and in the goat it should be shorter than the lateral process. However it was not so for the Soay calcanei or for the small sample of goat bones from Holy Island. In these samples this proportion was found to be too variable to be distinctive. (See Appendix for summaries of measurements).

Metapodial bones

In the sheep and goat, as in all two-toed ruminants, the third and fourth metacarpal and metatarsal (metapodial) bones are extended in length and fused to form a single shaft with two distal condyles. These articulate with the phalanges which carry the two hooves on each foot. In the foetus, however, the two shafts of the metapodial bones are unfused and can be seen to be separate elements.

The proximal end of the metacarpal bone articulates with the distal ends of the carpal bones, forming the knee joint in the forelimb. The proximal end of the metatarsal bone articulates with the distal ends of the tarsal bones in the hock joint of the hindlimb.

In the wild sheep (*Ovis orientalis*) the metapodial bones are

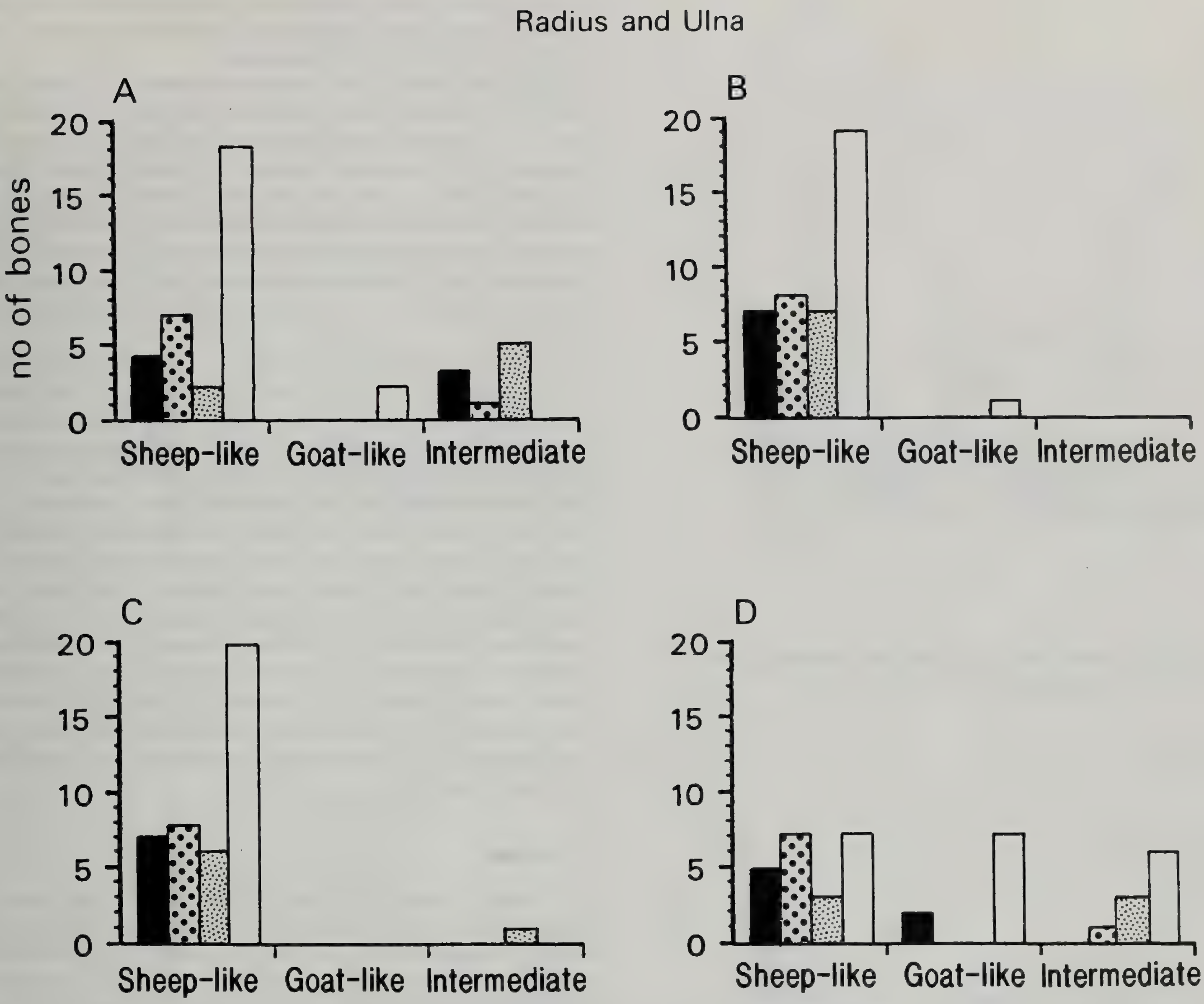


Fig. 21 Radius and ulna: analysis of sheep-like & goat-like characters. A fusion of shafts of radius and ulna: sheep—unfused; goat—fused proximally. B shape of lateral edge of proximal articular surface of radius: sheep—forms a ledge; goat—ledge absent. C shape of distal facet in radius for articulation with the scaphoid: sheep—long and narrow; goat—broad and more angular. D shape of medial edge of olecranon process of ulna: sheep—slightly convex; goat—almost straight.

long and rather like those of deer in their proportions, while in the goat the metapodial bones are shorter and more robust, especially in the metacarpal of the wild male goat (*Capra aegagrus*). These proportional differences make the wild sheep a longer-limbed, more deer-like animal than the wild goat. In the domestic caprines, however, the proportional differences have been reversed by artificial selection for short-legged sheep in north western Europe, so that in Britain goats are generally taller animals than sheep. On the other hand the bones of a castrated ram grow longer than those of the entire male so wethers will be taller than ewes or rams.

As the Soay sheep has not been subjected to artificial selection for perhaps thousands of years the body and limbs, particularly the metapodials, are relatively longer than they are in domestic breeds but they closely resemble those of early domestic sheep whose remains are found on prehistoric sites, and they are considerably longer for their width than the metapodial bones of the goat.

The mean lengths of the combined samples of male and female metapodial bones are 116.75 (metacarpals) and 126.57 (metatarsals); for the castrates the mean lengths are 127.54 (metacarpals) and 140.58 (metatarsals); and for the goats the mean lengths are 121.32 (metacarpals) and 133.05 (metatarsals).

The proximal epiphyses of the metapodial bones fuse before birth as do the two shafts of each bone. The distal epiphyses, which at first are two separate condyles, fuse between 18–24 months, according to Silver (1969). However in the sample of Soays the one castrate of 2 years 1 month has unfused metapodial condyles and amongst the three year old males and females only four are fused (Fig. 2).

It is rather easy to distinguish the complete metapodial bones of the Soay from those of the goat by their long slender proportions although, as already stated, this does not hold good for improved breeds of sheep. If the width of the shaft is expressed as a percentage of the length of the bone then this index was never more than 13% for the Soay metacarpal and 11% for the metatarsal, while for the goat the indices were always more than 17% for the metacarpal and 12% for the metatarsal (see Appendix for summaries of the measurements).

The proximal ends of the metapodial bones are difficult to distinguish between sheep and goat, but this can sometimes be done by the presence or absence of synovial pits in the

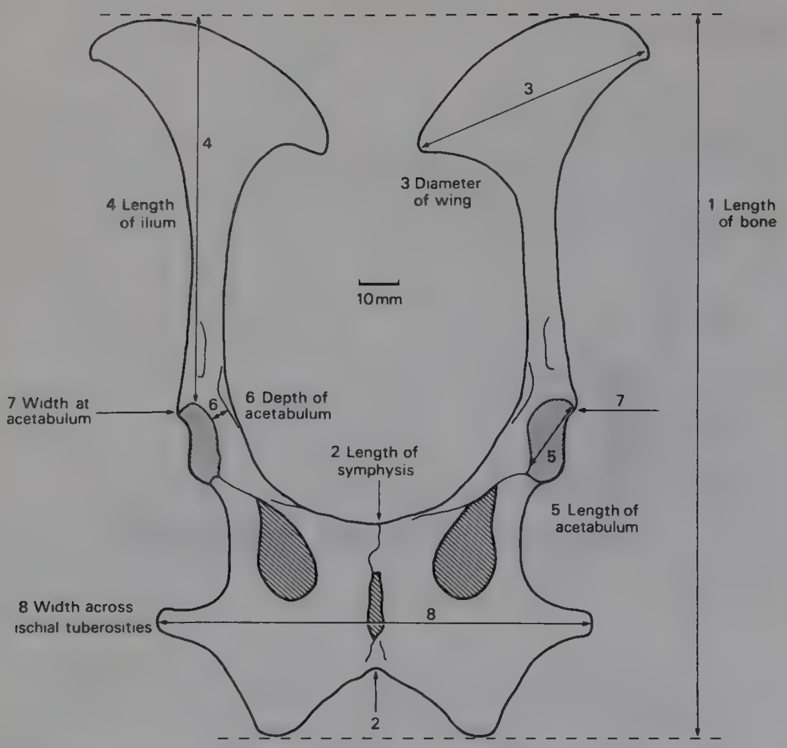


Fig. 22 Pelvis: ventral view of left and right innominate bones. 1–8 measurements (see Appendix).

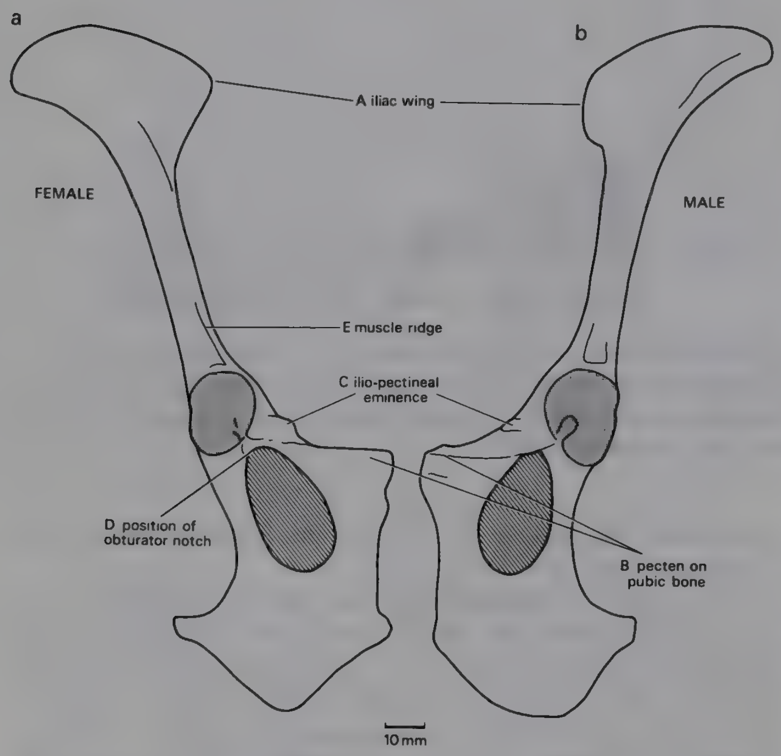


Fig. 23 Pelvis: **a** female—ventral view of right innominate bone. **b** male—ventral view of left innominate bone. A—E characters analysed in Figure 24.

articular surface (Fig. 30c A, d A). (Synovial pits or fossae are non-articular cavities in the surface of a bone which forms part of a synovial joint). Boessneck (1969) claimed that pits are rare in metacarpal bones but that they are sometimes found in goats. However, amongst the metacarpals of the Soays a high proportion have synovial pits (Fig. 31 A). In the metatarsal the situation is more complicated: in the sheep, according to Boessneck (1969) there should be no synovial pits but if present there should be only one circular hole. In the goat on the other hand there are often from one to three strikingly large holes. Figure 31 A shows that this character is consistent for the proximal ends of the Soay metatarsal bones and there are no intermediate cases.

The distal ends of the metapodial bones are rather easier than the proximal ends to distinguish between sheep and goat. As described by Boessneck (1969) the two verticilli (whorls) of the trochlear condyles lie parallel to each other in the sheep while in the goat the medial verticillus diverges at an acute angle from the lateral verticillus (Fig. 30a B, b B). In the Soay metacarpals and metatarsals this character is fairly consistent but in both elements there are some intermediate conditions where the verticillus was at a slight angle (Fig. 31 B, B).

A second distinction in the distal condyles is determined by measurement. In the sheep the parts of the condyle peripheral to the verticilli are larger and less deeply notched than in the goat (Fig. 30e), although this is more marked in the metacarpal than in the metatarsal, and the medial trochlear condyle is larger than the lateral. If the diameter of the medial trochlear condyle is measured against the diameter of the medial verticillus (the distal depth of the condyle) the index is found to be significantly higher in the sheep metacarpal than in the goat and marginally higher in the sheep metatarsal. The index for the metacarpals of the Soay sample is never below 62% and never above 62% for the goat which agrees with the results of Boessneck (1969). The indices for the metatarsal are a minimum of 60.6% for the Soays and a maximum of 60.7% for the goat (see Appendix for summaries of measurements).

Phalanges

The sheep conforms to the normal mammalian pattern of three phalanges in each functional digit in the fore and hind limbs. The proximal end of the first phalanx articulates with the distal end of the metapodial bone and is commonly known as the fetlock, while the joint between the first and second phalanges is known as the pastern. (The third joint between the second phalanx and the hoof used to be called, in the horse, the coffin joint). There are sesamoid bones on the posterior sides at the distal ends of the metapodial bones, phalanx 1, and phalanx 2.

It is not easy in the sheep to distinguish the phalanges of the fore and hindlimb although phalanx 1 is often longer and more robust in the forelimb than it is in the hind, especially in male animals carrying heavy horns. It is relatively easy to distinguish the phalanges of sheep from those of goat on the characters described by Boessneck (1969).

PHALANX 1. The mean length of the combined male and female, fore and hind limb first phalanges of the Soays is 32.94, for the castrates it is 34.80 and for the goat it is 43.91.

In Silver (1969) there is a misprint in the table giving the fusion times of the ox and sheep first phalanges. The ages are transposed so that the proximal epiphyses should read 13–16 months (1½ years in the ox) and the distal epiphyses should read before birth for both sheep and ox instead of vice versa. In the sample of Soays the proximal epiphysis is beginning to fuse in some of the one year olds and is fully fused in all the older specimens (Fig. 2).

There are four characters that distinguish the first phalanges of sheep from those of goat. At the proximal end of the bone, in the sheep, the lateral edge of the posterior side of the bone below the proximal articular surface does not form a

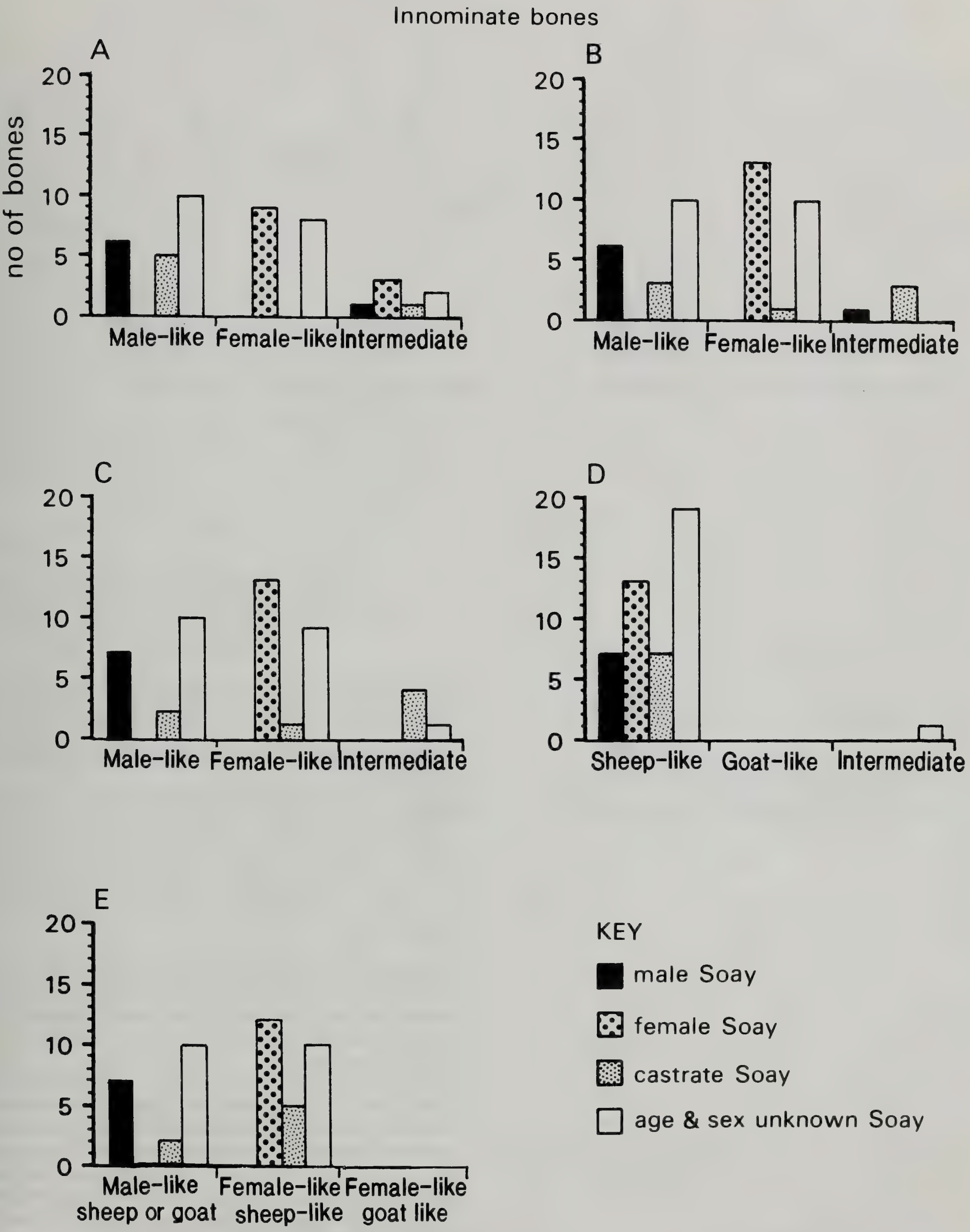


Fig. 24 Pelvis: analysis of male-like & female-like and sheep-like & goat-like characters. A shape of iliac wing: male sheep and goat—blunt and rounded; female sheep and goat—pointed. B shape of pecten: male sheep and goat—rounded and indistinct on robust pubic bone; female sheep and goat—a sharp ridge on slender pubic bone. C shape of iliopectineal eminence on pubic bone: male sheep and goat—pad-shaped; female sheep and goat—sharp-edged or pointed. D notch on anterior, dorsal border of obturator foramen: sheep—absent; goat—present. E muscle ridge on ventral body of ilium: male sheep and goat—absent; female sheep—short, narrow ridge bordering and deep pit; female goat—long, more strongly-marked ridge, shallow pit.

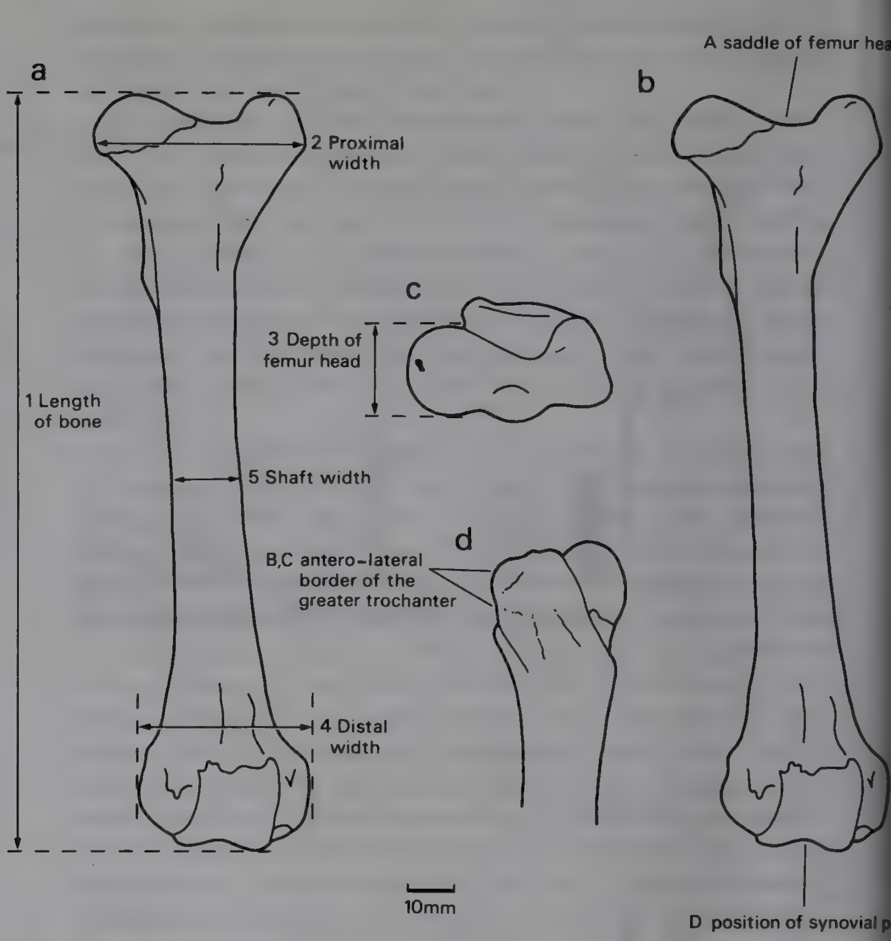

a
2 Proximal width
1 Length of bone
c
3 Depth of femur head
5 Shaft width
d
B,C antero-lateral border of the greater trochanter
4 Distal width
10mm
b
A saddle of femur hea
D position of synovial p

Fig 25 Left femur. **a** and **b** anterior views. **c** dorsal view of proximal articular surface. **d** lateral view of proximal end. 1–5 measurements (see Appendix). A–D characters analysed in Figure 27.

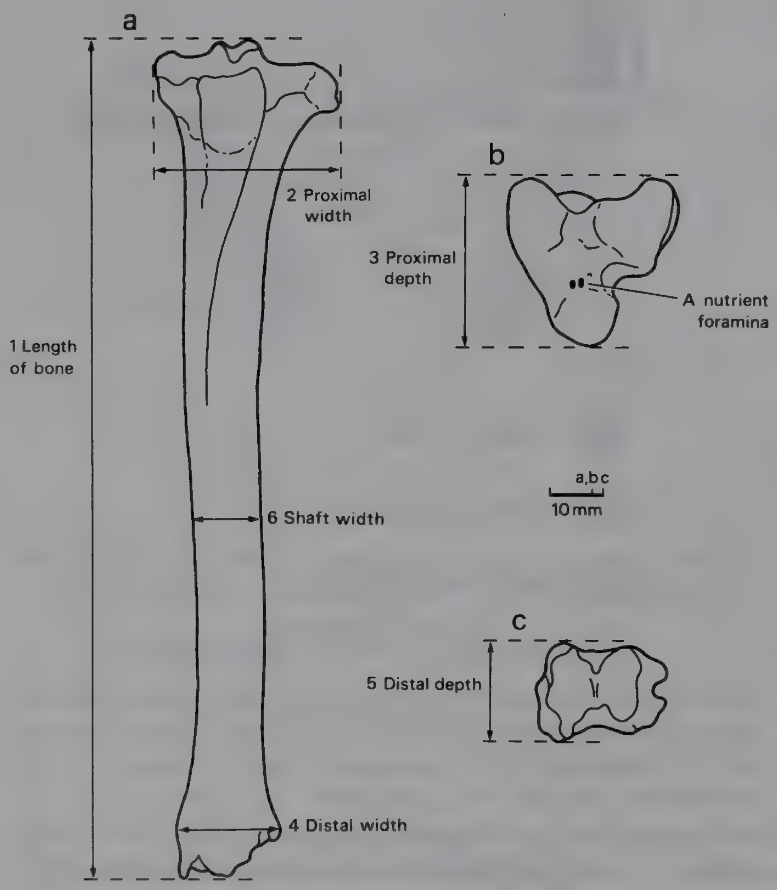

a
2 Proximal width
1 Length of bone
6 Shaft width
4 Distal width
b
3 Proximal depth
A nutrient foramina
a,bc
10mm
c
5 Distal depth

Fig 26 Left tibia: **a** anterior view. **b** dorsal view of proximal articular surface. **c** ventral view of distal articular surface. 1–6 measurements (see Appendix). A, B characters analysed in Figure 27.

ridge as it does in the goat (Fig. 32b A, d A). However this ridge was found difficult to assess and it can be seen from the results in Figure 33 A that there is a high proportion of phalanges that are either intermediate or goat-like for this character.

The most clear-cut differences were seen in the flat or slightly convex surface of the posterior side of the phalanx (usually concave in the goat) (Figs 32b B, 33 B), the poorly-marked muscle scars on the edges of the posterior side (Figs 32b C, d C, 33c), and most obviously the wide angle of the two halves of the posterior, distal articular surface (Figs 32b D, 33 D).

PHALANX 2. The second phalanx is about two thirds the length of the first. The mean length of the combined male and female, fore and hindlimb second phalanges of the Soays is 20.09, for the castrates it is 20.47 and for the goat it is 31.06, (Fig. 32f; Appendix).

As with the first phalanx there is a transposition of the fusion ages for the proximal and distal epiphyses in the table of Silver (1969). The ages should read 13–16 months for the proximal epiphysis (1½ years for the ox) and before birth for the distal epiphysis. As with the first phalanx, the proximal epiphyses of the Soay second phalanges were beginning to fuse in the one year old elements and were fully fused in the older specimens (Fig. 2).

There is one clear distinction between the second phalanges of sheep and goat. In the sheep, including Soays, the two halves of the posterior, distal articular surface are similar in size while in the goat the medial side is drawn up into a ridge or little 'tail' (Fig. 32g A). Figure 33 A shows that only

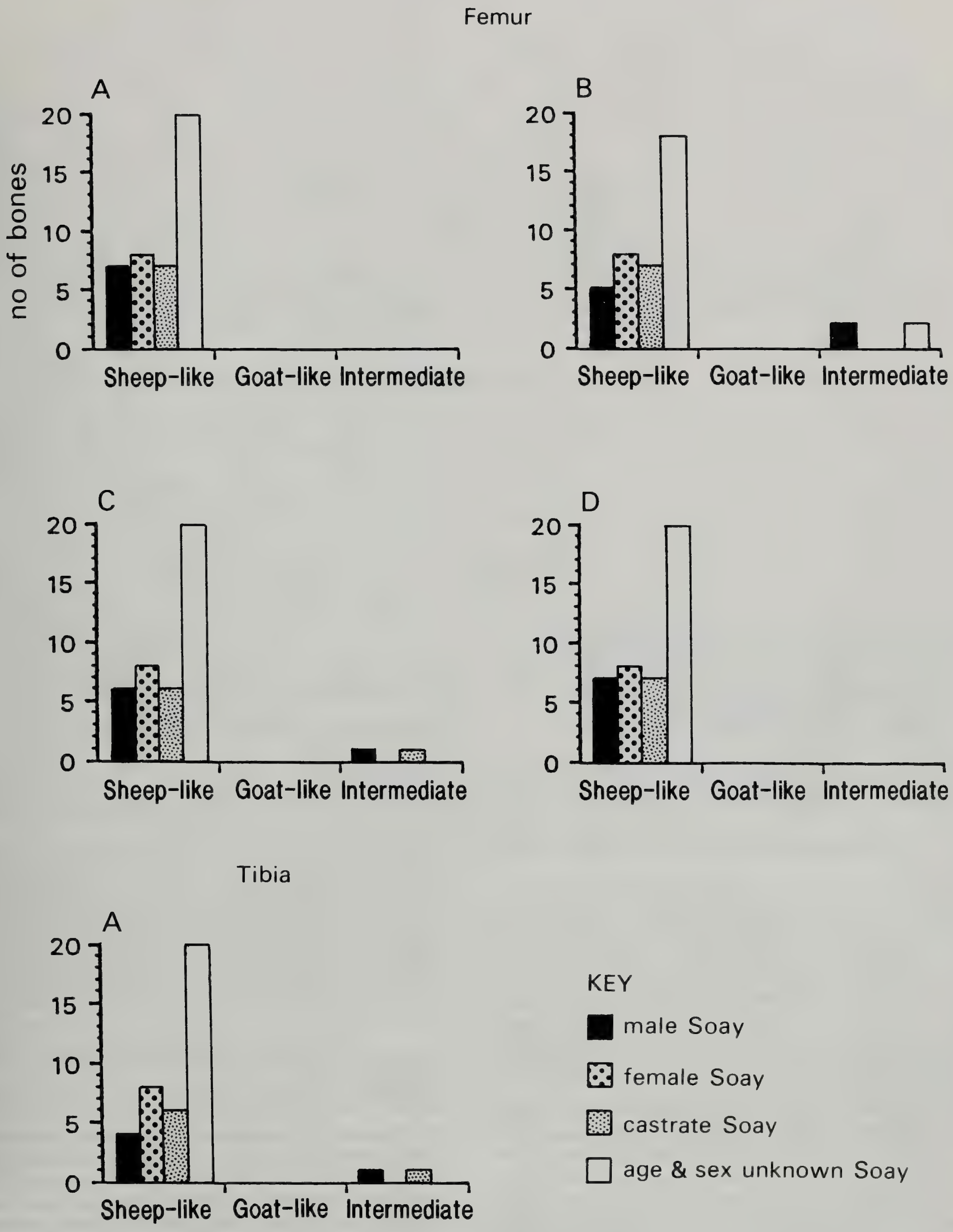


Fig. 27 Femur and tibia: analysis of sheep-like & goat-like characters. Femur A shape of head: sheep—extended in a medio-lateral direction across the saddle of the proximal end: goat—restricted and ball-like. B shape of antero-lateral border of greater trochanter: sheep—flat or with shallow depression; goat—slightly convex. C profile of antero-lateral border: sheep—square; goat—rounded. D synovial pit on distal trochlear: sheep—absent; goat—present. Tibia A position of nutrient foramina on proximal articular surface: sheep—one or more foramina on flat surface of epiphysis; goat—foramina are contained in a pit.

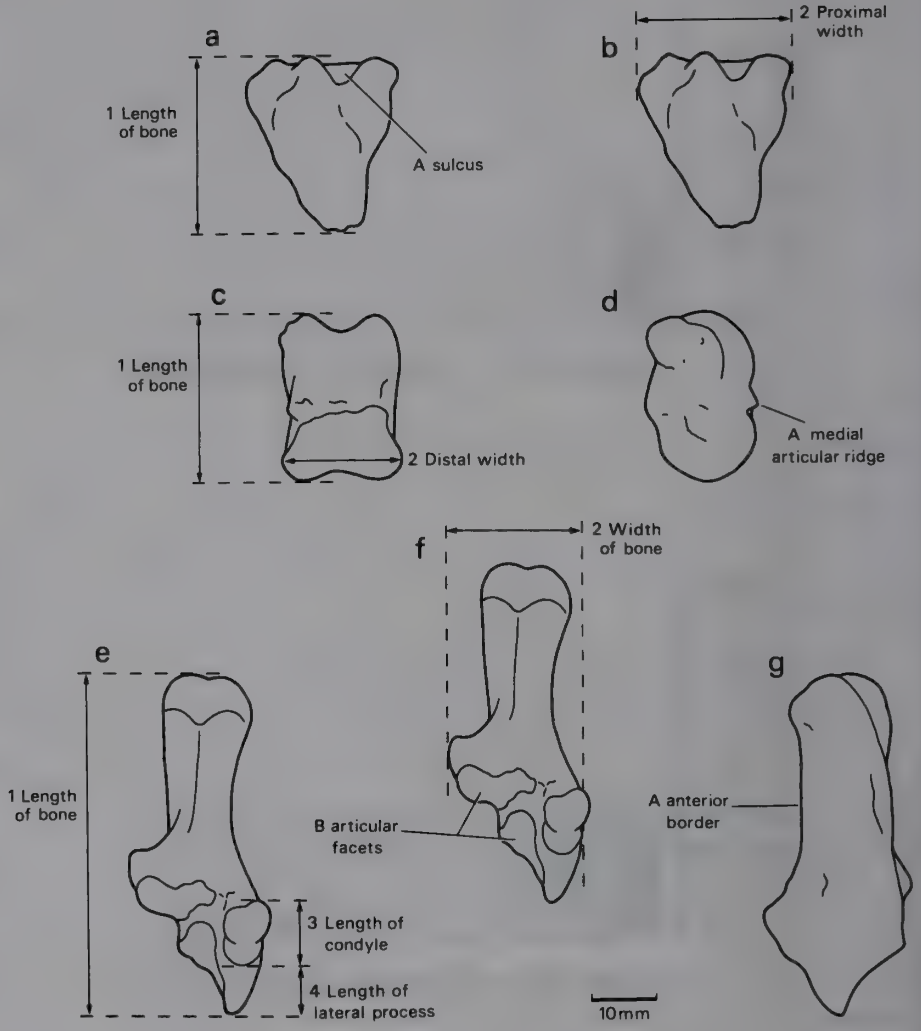


Fig. 28 Left patella, talus and calcaneum: **a** and **b** anterior view of patella. 1 and 2 measurements (see Appendix). A character analysed in Figure 29. **c** anterior view of talus. 1 and 2 measurements (see Appendix). **d** medial view of talus. A character analysed in Figure 29. **e** and **f** dorsal views of calcaneum. 1–4 measurements (see Appendix). B character analysed in Figure 29. **g** lateral view of calcaneum. A character analysed in Figure 29.

two of the Soay second phalanges are intermediate for this character.

PHALANX 3—HOOF CORE. The third phalanx is quite different in shape from the other two because it forms a core for the hoof. Its lateral side is rough, porous, and perforated by foramina while its medial side is flattened to lie as a pair against the adjacent hoof. The sole of the hoof core is slender and slightly twisted. The length of the bone is measured along the sole (Fig. 34a 1). The mean length of the combined male and female hoof cores of the Soays is 24.96, for the castrates it is 27.64, and for the goats it is 33.41.

The bone has no epiphysis and is partly ossified at birth which explains why newborn sheep and other hoofed mammals have very large feet for their overall size at birth.

The hoof core of sheep is easily distinguished from that of the goat, in which it is a narrower and sharper bone. Four characters were used in the analysis of the Soays, of which all but the first proved to be sound. The round blunt dorsal edge of the bone, as described by Boessneck for sheep is not seen clearly in the Soay hoof cores (Figs 34b A, 35 A) and it may be that these sheep have narrower hooves than the improved breeds, in adaptation to their rocky environment. A small proportion of hoof cores is intermediate for the second character which is a larger extensor process coming down into a hollow or saddle, whereas in the goat the profile is continuous and convex (Figs 34b B, 35 B). The third and fourth characters, which are a convex lateral edge to the sole and a concave medial edge are consistent discriminants with only one element being intermediate (Figs 34a C, a D, 35 C D).

DISCUSSION

The purpose of this work is to provide a comprehensive description of the skeleton of a single breed of sheep with a set of measurements for each skeletal element and to test the criteria for distinguishing sheep bones from goat bones in material from archaeological sites. In addition the effects of castration in the male have been investigated.

The distinction between sheep and goat remains on archaeological sites is of considerable importance for the interpretation of the palaeoeconomy and palaeoecology of the site. For example from the Neolithic site of the Links of Noltland on

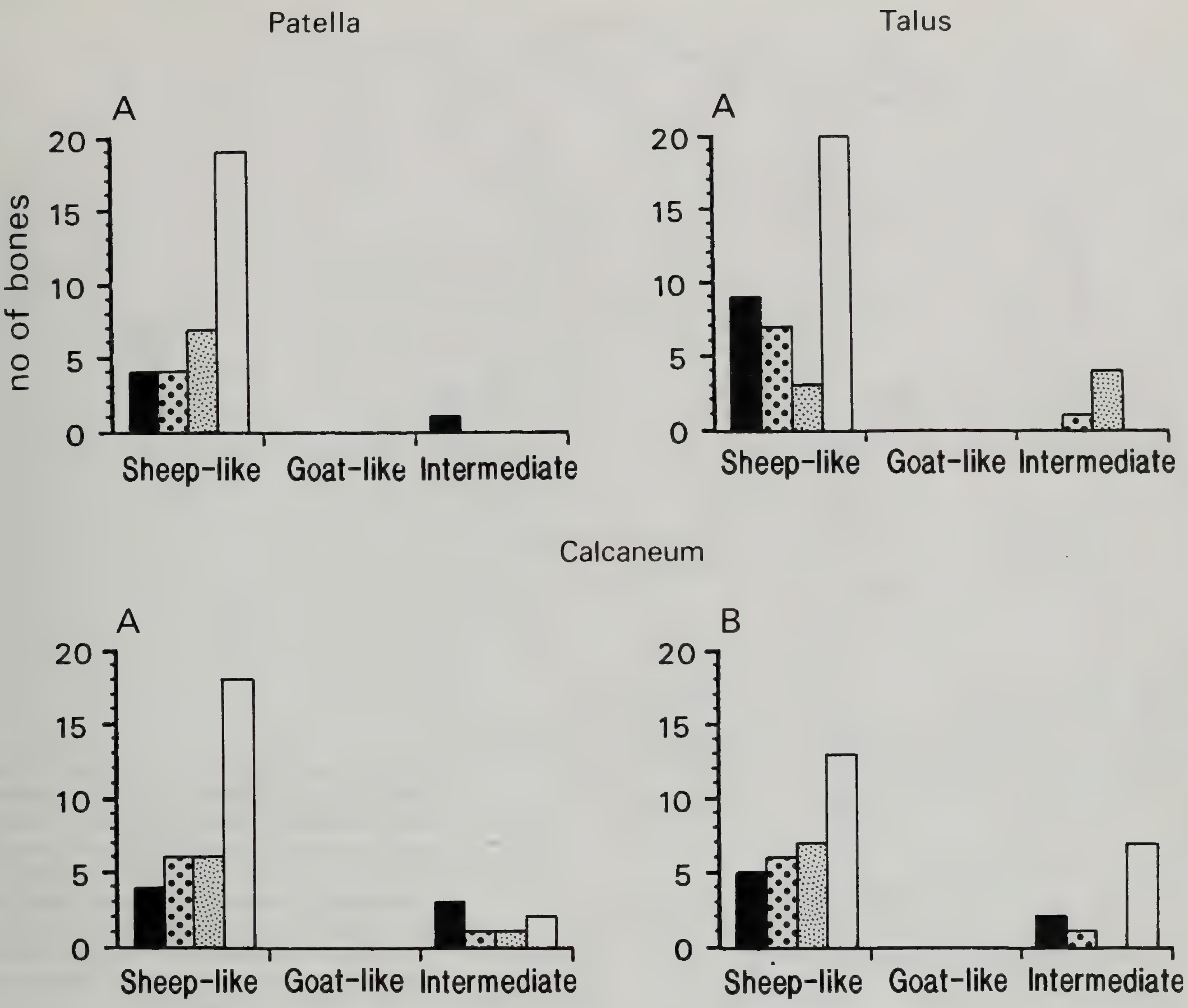


Fig. 29 Patella, talus, and calcaneum: analysis of sheep-like and goat-like characters. Patella: A sulcus on antero-proximal side: sheep—present; goat—absent or small. Talus: A shape of distal end of medial articular ridge: sheep—weakly developed and without a sharp angle; goat—drawn into a point and strongly developed. Calcaneum: A shape of anterior border: sheep—straight; goat—convex. B shape of articular facets for the posterior side of the talus: sheep—separated into two parts; goat—a single facet.

the island of Westray, Orkney, no goat remains have been identified; the economy was unusual for the Neolithic in being based mostly on sheep with a few cattle, pigs, and red deer adding to the meat-supply, which was also supplemented by fish and perhaps some whale and seal meat (Armour-Chelu, in prep.). There is no evidence (such as artefacts for spinning or weaving) for the use of wool from these Neolithic sheep but they may have been milked.

From another Neolithic site, that of Yvonand IV, a typical lake village site on the shore of Lake Neuchâtel in Switzerland, 5021 elements were identified to species. There were 66 bones of sheep (1.3% of the total number of identified elements); 35 bones of goat (0.7%); and 184 elements that were sheep or goat (3.7%). So here, it seems there were approximately twice as many sheep as goats but caprines as a whole were an insignificant part of the meat-supply which was mostly obtained from cattle and pigs, as is usual for the Neolithic in Europe (Clutton-Brock, 1990).

In contrast, Neolithic sites in western Asia usually provide a preponderance of sheep and goat remains over other livestock, and goats are usually in greater numbers than sheep.

Although the aim should be to discriminate between as many elements of sheep and goat as possible, from any site there will always be a very large number of fragments that can only be ascribed to the category ‘sheep or goat’ because the characters for distinction will be broken away.

Sometimes it is possible to interpret details of human social life or tradition from the proportions of the different taxa represented by the animal remains. For example in the Middle Bronze Age at the famous site of Jericho (Israel) the great majority of the bones from the Tell (the habitation site) were from goats, whereas those from the tombs were from sheep which may have been considered as higher-status animals only to be killed for sacrifices (Clutton-Brock, in prep).

The work of Boessneck *et al.* (1964) on several hundred skeletons of sheep and goats has shown that the improved breeds retain their generic characteristics, but the size and proportions of the bones have been greatly altered by selective breeding.

The wild ancestor of all domestic sheep (*Ovis orientalis*) is a long-legged, fine-limbed artiodactyl, more deer-like and with

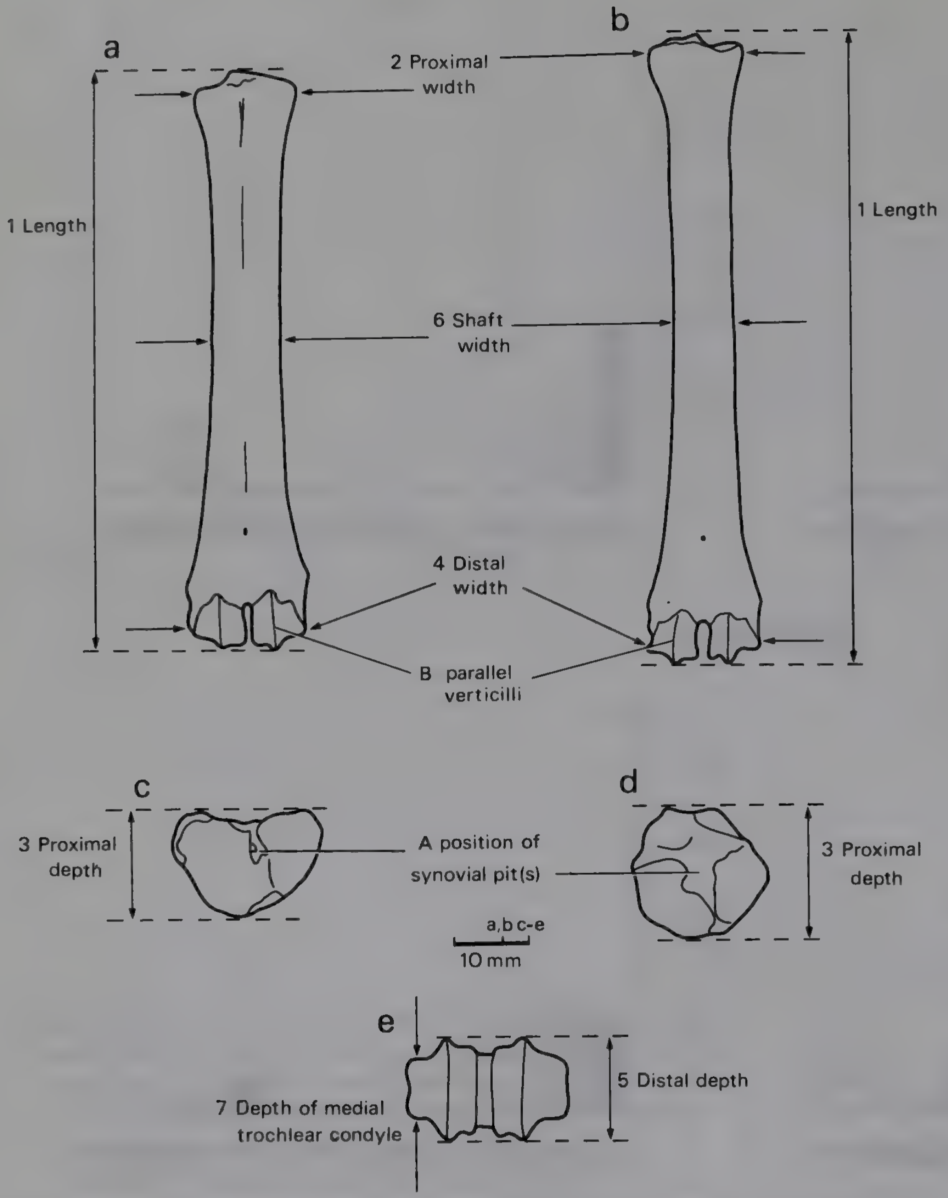


Fig. 30 Left metapodial bones: **a** and **b** anterior views of metacarpal and metatarsal. 1, 2, 4, 6 measurements (see Appendix). B character analysed in Figure 31 (metacarpal B and metatarsal B). **c** and **d** dorsal views of anterior articular surface of metacarpal and metatarsal. 3 measurement (see Appendix). A character analysed in Figure 31 (metacarpal A and metatarsal A). **e** ventral view of distal articular condyles of metacarpal/metatarsal. 5, 7 measurements (see Appendix).

longer limbs than the wild ancestor of the domestic goat (*Capra aegagrus*). Modern north European sheep have a barrel-shaped body and short thick-set limbs that are usually shorter than those of domestic goats which have been less influenced by artificial selection for meat quality. Because of these changes in the skeleton of the improved breeds of sheep it has been usual, since the time of Pitt-Rivers (1899), to use the Soay as a model of primitive domestic sheep for comparison with the remains of prehistoric sheep. Despite this use, no metrical or morphological analysis of the Soay has ever been undertaken until the present work.

We have found that although the Soay is a small fine-limbed sheep the legs are relatively and absolutely shorter than they were in the Neolithic sheep from the Links of Noltland on Westray, Orkney. This can be seen from Table 8 which gives the dimensions of the complete radii, metacarpals, and metatarsals from Noltland to compare with the dimensions of the same bones from the Soays, presented in the Appendix.

Two explanations for the shorter legs of the Soay may be suggested: either, these sheep had reached a later stage in domestication than the Noltland sheep before they were taken to the islands of St Kilda, or the shortening of the legs has occurred as a secondary adaptation to the particular selective pressures associated with survival on small islands.

In this context it is of interest to look at the work of Groves (1989) and Pees & Hemmer (1980) on the cranial capacities of living sheep. They found that the cranial capacity of the wild *Ovis orientalis* was slightly higher than that of the Corsico-Sardinian mouflon (*Ovis musimon*) which in turn was higher than the cranial capacity of domestic breeds. The Soay fell into the range of domestic sheep. This was to be expected as wild species normally have a higher cranial capacity than their domestic counterparts, and it is now generally accepted that the Corsico-Sardinian mouflon is an anciently feral sheep descended from very early domestic stock taken to the Mediterranean region from western Asia sometime around 7500 years ago (Geddes, 1984; Poplin, 1979). These sheep are closer to the wild *Ovis orientalis* than is the Soay not only in their cranial capacity but also in their longer limbs and in their wild-type pelage (see p. 3).

The conclusions that can be drawn from our very careful assessment of the characters of Boessneck *et al.* (1984) and Boessneck (1969) for the discrimination of sheep from goat bones are that there are very few characters, used on their own, on which a valid separation can be made. The following list of characters are those which, in the analysis presented here, fall only into the sheep-like category with no goat-like or intermediate specimens:

skull—presence of a lacrimal fossa; axis vertebra—presence

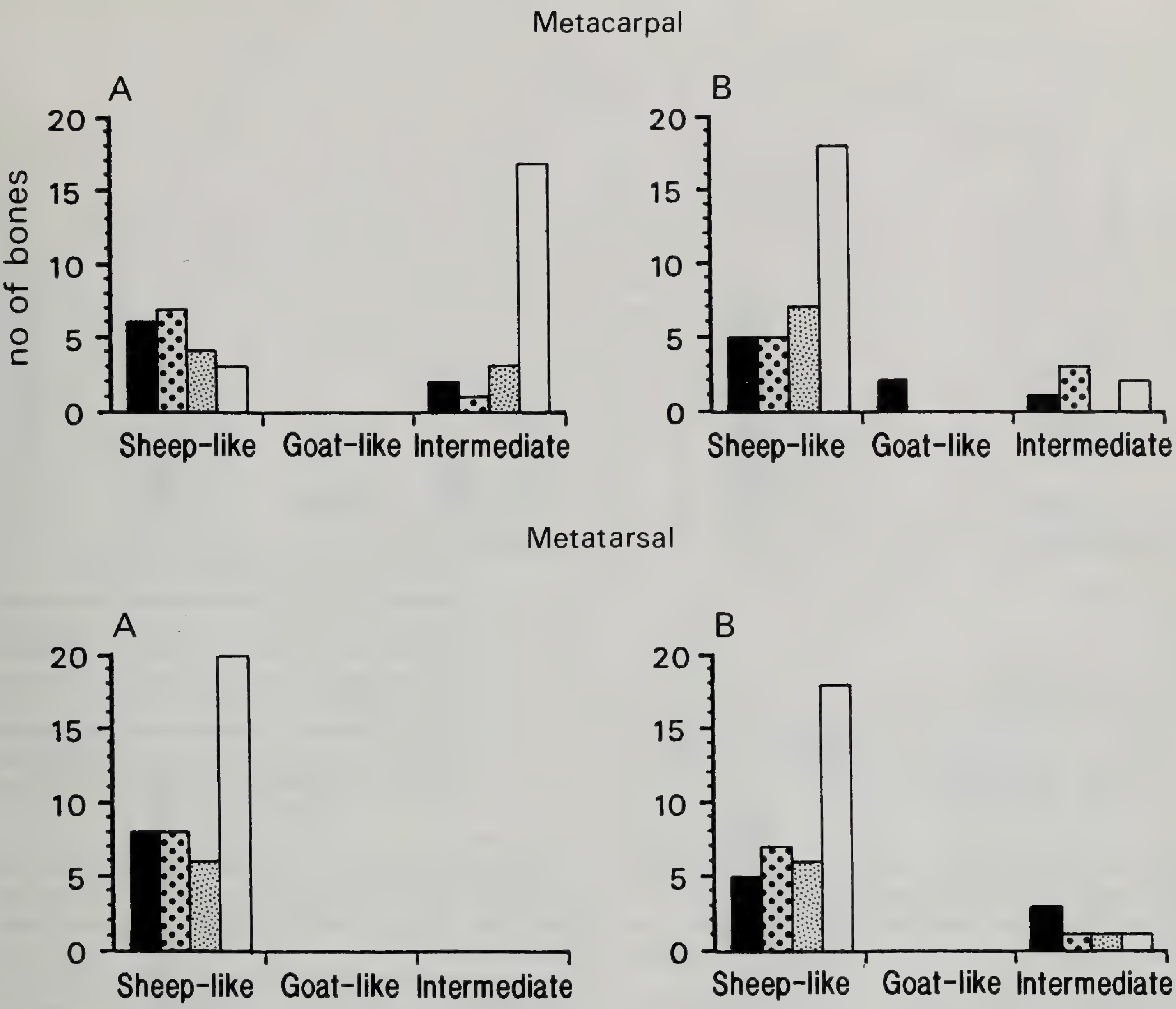


Fig. 31 Metapodial bones: analysis of sheep-like & goat-like characters. A Synovial pits on the proximal articular surface: sheep—absent in the metacarpal, rare in the metatarsal or if present there is one large circular hole; goat—sometimes present in the metacarpal, often present in the metatarsal. B angle of the verticilli of the distal condyles: sheep—lie parallel to each other in metacarpal and metatarsal; goat—the medial verticillus lies at an acute angle to the lateral verticillus in metacarpal and metatarsal.

of a transverse canal; scapula—concave anterior margin; femur—the head forms a continuum with the saddle at the proximal end and there are no synovial pits in the distal end; metatarsal—no synovial pit in the proximal end or if present only one circular hole; hoof core—concave profile to the medial edge of the sole.

It has long been held by archaeozoologists that many features of sheep bones, in addition to those mentioned above, are diagnostic. In the Soays, however, these are compromised by a few indeterminate examples. The features in question are as follows:

SKULL: the distinctive Y-shape of the frontal-parietal suture is not seen in one skull; the lambdoid suture is not straight but is intermediate in several skulls; and the temporal fossae are not convincingly wide apart in four skulls.

SCAPULA: the presence of a pecten on the posterior margin should be diagnostic of sheep; while no Soay scapulae are allocated as goat-like, four bones are intermediate.

HUMERUS: usually regarded as a particularly distinctive bone for each species; at the proximal end the lateral tuberosity should be broad and upright but three castrates are equivocal; the nutrient foramen should be at the back of the shaft but several are in the goat-like position on the side and two are intermediate; at the distal end the rounded epicondyle is usually considered to be one of the best sheep-like characters but two bones are intermediate.

RADIUS AND ULNA: these bones are usually unfused in the sheep and fused at the proximal ends of the shafts in the goat, but this distinction does not hold for a considerable number of the Soay elements one of which is fused and several are intermediate; the little ledge on the lateral border of the proximal end of the radius should be a diagnostic feature of sheep but it is absent in one bone.

PELVIS: the obdurator foramen should have no notch at its anterior end in the sheep but there is a slight notch in one Soay specimen.

FEMUR: the greater trochanter on the proximal epiphysis usually has a flat top and a square edge in the sheep but a few Soays are intermediate between sheep and goat for this character.

TALUS: in the sheep the medial articular ridge should be only

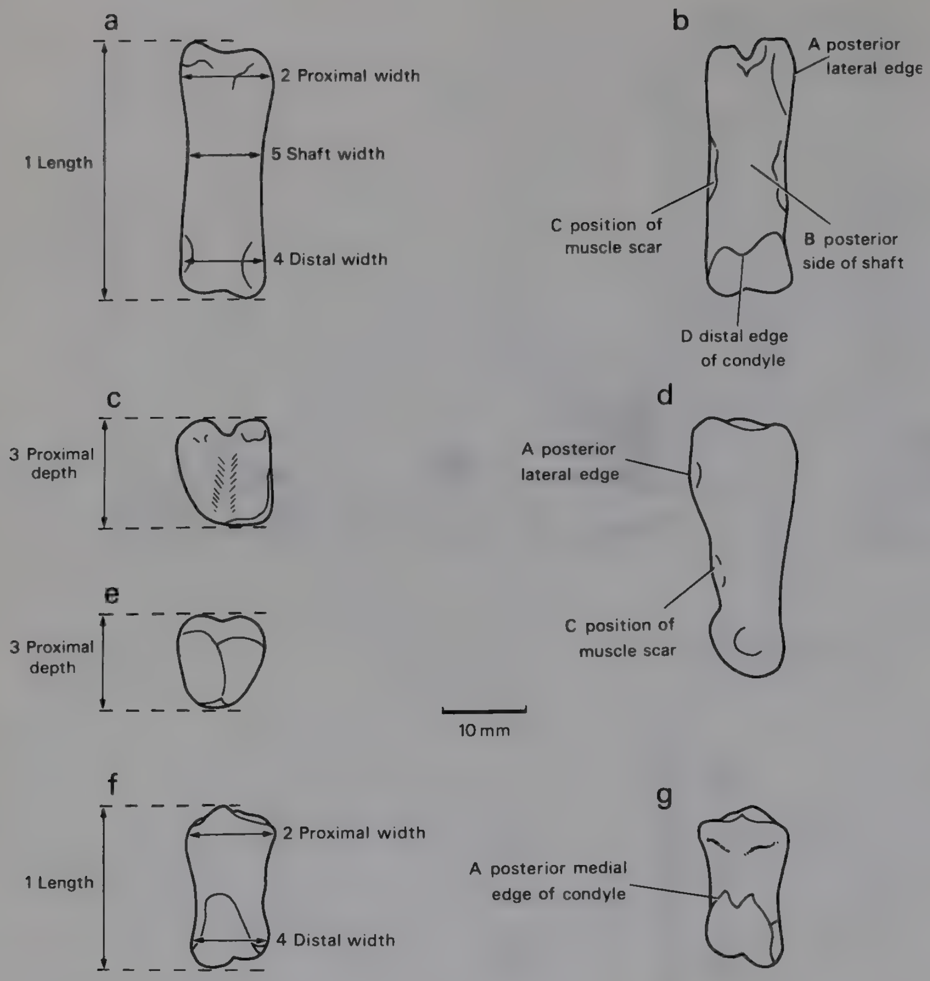


Fig. 32 Fore/hind phalanx 1 and 2: **a** anterior view of phalanx 1. 1, 2, 4, 5 measurements (see Appendix). **b** posterior view of phalanx 1; **d** lateral view of phalanx 1. A—D characters analysed in Figure 33. **c** dorsal view of proximal articular surface of phalanx 1. 3 measurement (see Appendix). **e** dorsal view of proximal articular surface of phalanx 2. 3 measurement (see Appendix). **f** anterior view of phalanx 2. 1, 2, 4 measurements (see Appendix). g posterior view of phalanx 2. A character analysed in Figure 33.

a weakly-developed bump but in five bones it is pointed enough for them to be classed as intermediate.

Calcaneum: the articular facets are said to be separate in the sheep but a number of the Soay elements exhibit some degree of fusion.

Metapodial bones: the verticilli on the distal condyles are expected to be parallel to each other in the sheep while in the goat the medial verticillus diverges, but in one Soay this character is goat-like and in a number it is intermediate.

Phalanx 1: the shape of this element is usually quite distinctive in the sheep and goat but in the Soays the discrimination is not clear-cut for several of the characters, which may be due to the particularly active life of these sheep.

Phalanx 2: the best character for discrimination is the symmetry of the posterior side of the distal condyle and this does apply well in the Soays except for two intermediates.

Phalanx 3 (hoof core): the distinctive features noted by Boessneck, the rounded dorsal edge and the development of the extensor process are not found in the Soays while the convex lateral edge is compromised by one intermediate hoof core.

Most of the measurement ratios quoted by Boessneck were tried out on the Soay bones but they were not all found to be good discriminants; those that are useful are discussed in the text.

Each character in the analysis was tested on the male, female, and castrate samples as well as on the elements of unknown sex. However, the sex of the elements does not appear to affect the discriminant features except that some are poorly defined in the castrates. To take one example, the shape of the lateral tuberosity at the proximal end of the humerus is generally considered to be a sound character for distinction and in the analysis all the bones fall into the sheep-like category except for three castrates which are intermediate.

Sex-related characters were examined in the atlas, axis, and pelvis. The atlas is less reliable as an indicator of sex or genus than expected and these vertebrae in the Soays exhibit all possible interpretations. On the other hand in the axis the development of the ventral crest is a good discriminant for male sheep but is not very useful because female sheep cannot be separated from female goats on this character. In the pelvis the shape of the iliac wing is a reliable determinant for the male Soays but is less so for the females. The sex difference in the shape of the pecten that develops on the pubic bone permits clear allocation to male or female but in the castrates the pecten is indeterminate. The ilio-pectineal eminence gives a reliable and absolute distinction between male and female but again it is intermediate in the castrates.

This analysis of the characters that are used to divide sheep bones from those of goats, and males from females, appears to show that many of the discriminants are unreliable but it should not be assumed that the task of separating the elements retrieved from archaeological excavation is too difficult to be attempted. When used in conjunction, and together with the proportional differences ascertained by measurement, it is possible to make specific identifications with a high degree of confidence.

A significant conclusion to be drawn from this osteological study concerns the age of skeletal maturity characterized by the complete fusion of the epiphyses in the limb bones (Fig. 2). Contrary to the widely-held theory that primitive breeds like the Soay are retarded in the times of epiphysial fusion

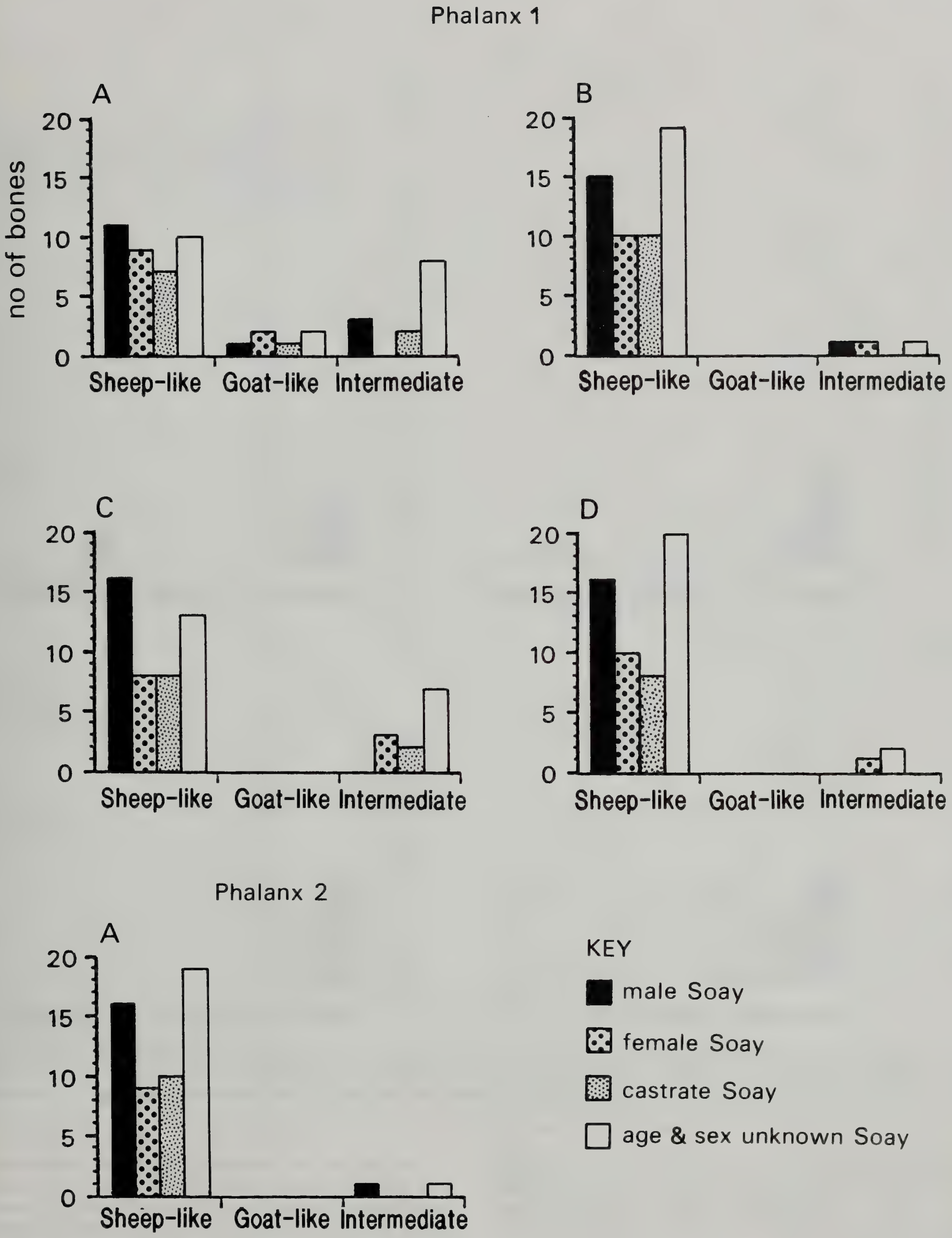


Fig. 33 Fore/hind phalanx 1 and 2: analysis of sheep-like & goat-like characters. Phalanx 1: A shape of lateral edge below proximal articular surface: sheep—rounded without a ridge; goat—forms a ridge. B shape of posterior side of shaft: sheep—flat or convex; goat—concave. C development of muscle scars on posterior mid-shaft: sheep—weak; goat—more strongly developed. D shape of posterior edge of distal articular condyle: sheep—has a wide open or obtuse angle; goat—has an acute or right angle. Phalanx 2: A shape of posterior medial edge of distal articular condyle: sheep—equal in height to the posterior lateral edge; goat—drawn up into a little tail.

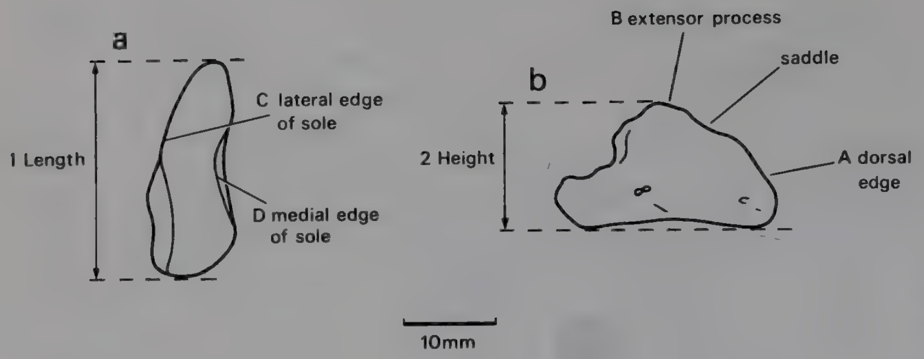


Fig. 34 Fore/hind phalanx 3 or hoof core: **a** ventral view. 1 measurement (see Appendix). C, D characters analysed in Figure 35. **b** lateral view. 2 measurement (see Appendix). A, B characters analysed in Figure 35.

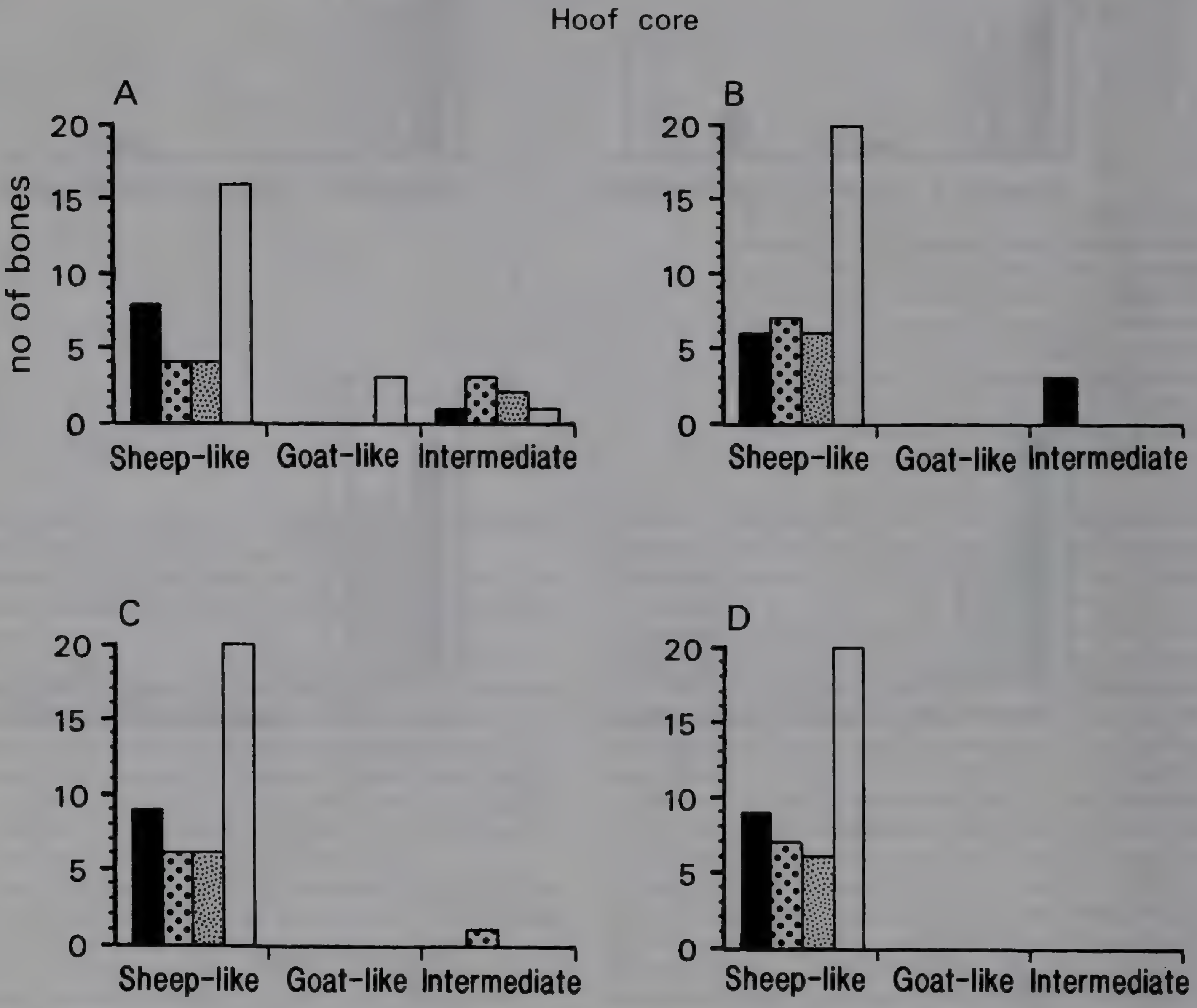


Fig. 35 Fore/hind phalanx 3 or hoof core: analysis of sheep-like & goat-like characters. A shape of dorsal edge: sheep—rounded and blunt; goat—medio-laterally flattened, sharp and pointed. B shape of extensor process: sheep—large and with a saddle or hollow in front of it; goat—small and with no saddle. C shape of lateral edge of sole: sheep—convex; goat—straight. D shape of medial edge of sole: sheep—concave; goat—straight.

compared with improved sheep, it has been found that the time of complete fusion (between three and three and a half years, see Fig. 2) is comparable to the time taken in breeds such as the Southdown that have been developed specially for early fattening.

It is interesting that another primitive breed, the Gotlandic sheep studied by Hatting (1983), also exhibited skeletal maturity at the unexpectedly early age of two and a half years.

From the work of Hammond (1940) and other researchers it is evident that the early livestock improvers and their successors, while shortening the limbs and altering the normal sequence in the development of fat and muscle, in no way affected the rate of skeletal development; so that in both improved and unimproved (including primitive) breeds of sheep epiphysial fusion takes place at the same ages. Viewed in this light, the findings of the present study, as well as those of Hatting, do not seem so anomalous. This has important

Table 8 Dimensions (in mm) of radii, metacarpals and metatarsals of sheep from the Neolithic site of the Links of Noltland, Westray, Orkney.

RADIUS		
1 Length of bone	No	16
	max	174.1
	min	131.38
	mean	149.73
	st.dev	10.98
2 Proximal width	No	16
	max	32.37
	min	26.82
	mean	30.03
	st.dev	1.51
3 Proximal depth	No	16
	max	16.82
	min	14.12
	mean	15.58
	st.dev	0.78
4 Distal width	No	16
	max	29.75
	min	24.66
	mean	27.41
	st. dev	1.51
5 Distal depth	No	16
	max	20.98
	min	16.57
	mean	18.41
	st.dev	1.22
6 Shaft width	No	16
	max	18.24
	min	13.24
	mean	16.1
	st.dev	1.29
METACARPAL		
1 Length of bone	No	13
	max	134.5
	min	112.62
	mean	125.57
	st. dev	6.29
2 Proximal width	No	12
	max	23.94
	min	19.96
	mean	21.56
	st.dev	0.95
3 Proximal depth	No	12
	max	16.92
	min	15.04
	mean	16.19
	st.dev	0.51
4 Distal width	No	12
	max	26.57
	min	22.06
	mean	25.02
	st.dev	1.22
5 Distal depth	No	13
	max	16.56
	min	13.3
	mean	15.45
	st.dev	0.86
6 Shaft width	No	12
	max	14.1
	min	11.28
	mean	12.7
	st.dev	0.82
7 Depth of medial trochlear condyle	No	13
	max	12.12
	min	10.22
	mean	11.50
	st.dev	0.54
METATARSAL		
1 Length of bone	No	12
	max	145.02
	min	125.68
	mean	135.00
	st.dev	6.26
2 Proximal width	No	12
	max	21.75
	min	16.86
	mean	18.88
	st.dev	1.5
3 Proximal depth	No	11
	max	21.2
	min	17.54
	mean	19.23
	st.dev	1.02
4 Distal width	No	12
	max	24.28
	min	20.72
	mean	22.58
	st.dev	0.96
5 Distal depth	No	12
	max	16.91
	min	14.48
	mean	15.55
	st.dev	0.77
6 Shaft width	No	12
	max	11.67
	min	10.08
	mean	10.49
	st.dev	0.55
7 Depth of medial trochlear condyle	No	12
	max	11.48
	min	8.16
	mean	10.26
	st.dev	0.92

implications for research into ancient practices of livestock husbandry, for it has been held that modern fusion data from improved breeds cannot be directly applied to the interpretation of sheep bones recovered from archaeological contexts earlier than the late 18th century. This view is contradicted by this study.

The collections of skeletal material from the carcasses of Soay sheep that had lived wild on the island of Hirta, St Kilda, provided the impetus for this study. Perhaps a main result has been to reveal how very many questions about the morphology and development of the skeletons of mammals still remain to be answered. Very little is known about the effects of castration on the skeleton and only very preliminary studies have been carried out on the side-effects of selection for meat-quality in sheep. For example the short report of Purser (1980) on the correlation between the shortening of the cannon bone (metacarpal) of the leg and reduction of prolificacy in ewes and fatness in wethers clearly requires further investigation. The skeletons of Soay sheep combined with data on their meat-quality and breeding success could provide a 'control' for such investigations.

It is intended that the summaries of measurements of the Soay bones and the analysis of the characters that distinguish sheep from goats, which are presented here, should be used as a data-base by archaeozoologists. The complete set of measurements are held as an archive in the British Museum (Natural History) and are available to research workers, on request, as are the collections of skeletal material for further direct study.

ACKNOWLEDGEMENTS. We are indebted to members of the Mammal Section at the British Museum (Natural History) and the Department of Veterinary Anatomy of Cambidge University who prepared and curated the skeletons of the Soay sheep for this project. The material was collected from Hirta, St. Kilda by Peter Jewell in the course of his field work which was assisted in part by grants from the Leverhulme Trust, the National Geographic Society and St. John's College, Cambridge, and by Philip Armitage in 1979 with the generous assistance of a grant from the Godman Exploration Fund through the British Museum (Natural History).

We should like to thank Sheila Cameron for collecting, preparing, and presenting to the BM(NH) the skeletal material of feral goats from Holy Island, Arran, and our thanks are also due to Valerie Hardman and Derek Harvey for help with collection of the data while they were employed at the museum on vacation studentships. We thank Miranda Armour-Chelu for help with measurements and for allowing us to publish her measurements of sheep limb bones from the site of the Links of Noltland, Westray, Orkney. We thank Sebastian Payne for his measurements of male Soays from Babraham, Cambridge.

Alan Patterson and Kay Shaw, Biometrics Section, BM(NH) assisted with the computer analysis of the measurements and Harry Taylor, photographic unit BM(NH), took the photographs. The manuscript was typed by Margaret Twinn in the Physiological Laboratory, University of Cambridge, and Mrs Dee Hughes helped with the lettering of the Figures.

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Manuscript accepted for publication 18 November, 1988

APPENDIX

Summaries of the measurements of skeletal elements of Soay sheep (*Ovis aries*) from Hirta, St. Kilda, Soay castrates from Cambridge, and feral goats (*Capra hircus*) from Holy Island, Arran, Scotland. The numbers that precede the description of each measurement refer to the dimension between the points depicted on each element in the Figures. All measurements are in mm.

HORNCORES

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male not aged	Soay Female not aged	Goat Male not aged	Goat Female not aged
No in sample		11	8	5	10	8	1	1
1 Length of outer curve of horn core	max	282.00	88.00	131.00	263.00	98.00	283.00	170.00
	min	164.00	65.00	5.10	162.00	12.00		
2 Basal circumference	max	166.00	82.00	106.00	143.00	82.00		
	min	102.00	68.00	60.10	127.80	34.00		

SKULL

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male not aged	Soay Female not aged	Goat Male not aged	Goat Female not aged
No in sample		12[1]	12[2]	6[3]	10[4]	13[5]	1	1
1 Condylo— basal length	max	206.40	203.60	225.60	209.90	216.00	–	216.90
	min	189.50	187.30	215.90	190.30	186.90		
	mean	197.99	195.07	220.42	198.14	195.91		
	st.dev	5.20	4.89	4.33	7.48	8.31		
2 Width across condyles	max	45.95	42.80	48.13	45.28	44.14	58.15	49.31
	min	38.87	37.71	42.56	36.08	37.70		
	mean	42.67	40.34	44.48	41.80	40.39		
	st.dev	1.99	1.63	2.31	3.10	1.85		
3 Cranial width	max	67.49	63.12	70.40	69.26	68.03	72.51	61.93
	min	58.54	55.59	50.03	60.59	59.38		
	mean	63.62	59.55	64.40	64.59	62.27		
	st.dev	2.51	2.29	6.91	2.66	2.71		
4 Zygomatic width	max	109.56	103.94	106.98	107.36	108.97	113.76	112.64
	min	85.73	93.33	101.52	90.12	93.61		
	mean	100.44	98.47	105.08	98.93	99.60		
	st.dev	7.96	3.45	2.12	5.14	4.60		
5 Width across orbits	max	81.90	74.02	78.27	86.00	75.36	88.31	80.24
	min	67.59	66.54	74.66	71.98	66.90		
	mean	75.60	70.11	76.27	77.62	70.94		
	st.dev	4.22	2.29	1.34	4.04	3.16		
6 Maxillary width	max	66.20	66.08	69.51	68.66	69.42	75.62	73.79
	min	58.81	58.61	63.56	62.03	59.25		
	mean	61.35	61.65	66.48	64.83	63.34		
	st.dev	2.55	2.30	2.17	2.48	3.15		
7 Premaxillary width	max	39.57	34.60	39.00	38.27	33.82	–	30.85
	min	31.59	27.83	35.02	30.42	27.11		
	mean	35.32	30.65	37.11	34.95	30.90		
	st.dev	2.74	2.17	1.43	2.61	1.87		
8 Palatal width	max	61.29	64.00	62.93	66.23	62.64	70.97	69.21
	min	55.61	55.76	60.03	57.18	56.58		
	mean	58.87	58.19	61.38	61.29	59.31		
	st.dev	2.12	2.25	1.03	2.63	1.80		

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male not aged	Soay Female not aged	Goat Male not aged	Goat Female not aged
No in sample		12[1]	12[2]	6[3]	10[4]	13[5]	1	1
9 Length of orbit	max	40.90	39.64	42.67	41.68	39.99	38.37	37.33
	min	37.00	37.25	39.34	37.81	37.18		
	mean	39.33	38.44	41.58	39.68	38.44		
	st.dev	1.42	0.80	1.24	1.20	0.93		
10 Height of orbit	max	40.05	40.57	39.39	40.01	38.71	37.61	33.77
	min	34.99	36.53	36.95	35.96	36.22		
	mean	37.60	37.90	38.19	37.87	37.75		
	st.dev	1.53	1.20	0.96	1.34	0.85		
11 length of toothrow (alveoli)	max	63.24	58.62	64.61	66.58	69.65	68.55	63.58
	min	53.83	50.22	56.99	52.18	53.03		
	mean	58.40	55.37	60.80	59.89	59.74		
	st.dev	3.15	2.20	3.01	4.24	5.27		
12 Height of back of skull	max	47.24	39.92	42.86	43.61	40.46	54.55	43.35
	min	39.46	36.78	38.86	39.86	34.96		
	mean	41.68	38.52	40.74	41.55	38.08		
	st.dev	2.05	0.84	1.69	1.43	1.62		
13 Width between bases of horn cores	max	40.88	45.64	51.80	43.70	58.84	29.67	36.15
	min	26.65	37.80	32.43	31.63	37.79		
	mean	34.64	41.55	41.30	36.77	44.71		
	st.dev	4.89	2.80	7.37	3.75	6.63		

1 10 in sample for condylo-basal length, premaxillary width and the width between the bases of the horn cores.
2 8 in sample for the width between the bases of the horn cores
3 7 in sample for cranial width, and width between the bases of the horn cores; 5 in sample for condylo-basal length and width across orbits.
4 7 in sample for condylo-basal length; 6 in sample for premaxillary width
5 11 in sample for condylo-basal length; 8 in sample for the width between the bases of the horn cores

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MANDIBLE

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		11	12	7	20[1]	3
1 Length from angle	max	157.10	159.50	173.40	166.10	186.70
	min	139.72	99.80	153.70	144.40	167.60
	mean	148.84	148.20	167.87	150.00	180.10
	st.dev	5.49	15.60	6.78	4.87	10.80
2 Length of horizontal ramus	max	109.60	105.96	120.05	118.87	133.11
	min	96.18	97.85	107.98	99.09	127.29
	mean	102.59	102.91	113.07	105.15	129.29
	st.dev	3.84	2.53	4.39	4.22	3.31
3 Length of cheektooth row	max	63.57	62.97	68.79	72.20	78.11
	min	56.63	55.23	58.36	56.63	72.35
	mean	60.17	59.34	64.06	62.65	75.30
	st.dev	2.22	2.27	4.36	3.42	2.88
4 Width of condyle	max	23.76	22.53	22.50	23.11	26.77
	min	19.26	19.18	17.44	18.06	24.21
	mean	21.39	20.88	20.26	20.73	25.13
	st.dev	1.39	0.98	1.61	1.33	1.43
5 Oral height of vertical ramus	max	90.78	94.40	98.11	93.88	108.27
	min	82.29	82.99	85.79	82.80	95.24
	mean	85.75	87.94	91.80	88.30	99.92
	st.dev	3.31	3.55	4.71	3.14	7.25
6 Height of mandible in front of M_1	max	20.80	19.34	22.54	20.66	23.85
	min	16.61	16.27	18.02	15.95	19.66
	mean	18.88	18.08	20.06	18.27	21.91
	st.dev	1.24	1.03	1.68	1.47	2.11

1 19 in sample for width of condyle

ATLAS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		12	8	7[1]	18[2]	2
1 Greatest length	max	53.91	51.74	53.05	55.83	76.74
	min	41.87	42.74	47.75	39.66	64.42
	mean	49.74	45.82	50.10	47.17	70.58
	st.dev	3.25	2.63	1.82	5.22	8.71
2 Greatest width over the wings	max	66.96	60.08	68.12	68.97	96.36
	min	48.75	52.69	53.85	45.86	83.70
	mean	62.08	55.46	62.05	58.06	90.03
	st.dev	5.05	3.04	6.01	7.22	8.95
3 Height of bone	max	36.19	32.46	35.63	36.64	46.05
	min	28.70	29.04	31.23	26.84	43.92
	mean	33.67	30.67	33.10	31.41	44.99
	st.dev	1.95	1.08	1.66	2.77	1.51
4 Width of cranial articular surface	max	46.18	43.01	48.33	46.61	65.51
	min	37.65	39.10	40.52	38.39	58.53
	mean	42.39	40.62	43.54	41.53	62.02
	st. dev	2.18	1.45	2.63	2.33	4.94
5 Width of caudal articular surface	max	44.34	38.82	45.47	43.97	57.77
	min	37.38	35.69	37.78	34.97	53.95
	mean	41.95	37.24	41.76	39.42	55.86
	st.dev	2.25	1.16	2.59	2.66	2.70
6 Ventral length along ventral tuberosity	max	24.42	22.94	24.37	24.56	33.89
	min	19.09	19.80	21.31	17.90	28.51
	mean	22.06	21.15	23.15	21.01	31.20
	st. dev	1.69	1.15	1.27	1.76	3.80

1 5 in sample for greatest width over the wings

2 17 in sample for greatest length and width of cranial articular surface; 16 in sample for greatest with over the wings.

AXIS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		10	6	7	19[1]	4[2]
1 Greatest height of bone	max	56.56	42.60	52.69	55.90	76.75
	min	47.69	40.65	42.36	33.54	65.04
	mean	52.26	41.58	49.08	42.26	69.87
	st.dev	2.78	0.65	3.38	6.67	5.27
2 Width of cranial articular surface	max	42.51	38.38	42.27	41.69	54.64
	min	38.05	35.46	37.19	34.57	49.87
	mean	40.64	36.60	39.32	37.94	51.88
	st.dev	1.57	1.25	1.99	2.11	1.99
3 Width of caudal articular surface	max	26.73	20.68	23.63	22.04	34.81
	min	20.46	18.63	18.61	15.24	27.79
	mean	22.82	19.59	21.72	19.56	31.05
	st.dev	2.65	0.84	1.58	1.82	2.99
4 Length including dens	max	52.85	53.84	56.70	5.55	70.10
	min	48.57	48.23	51.99	40.90	63.35
	mean	50.41	50.23	53.39	49.31	67.55
	st.dev	1.47	1.97	1.72	3.07	3.66
5 Length of spinous process	max	43.15	37.20	38.73	44.16	68.33
	min	35.38	31.88	31.77	24.93	58.75
	mean	38.27	33.93	35.84	33.75	62.74
	st.dev	2.46	1.94	2.87	4.19	4.02
6 Width of caudal end of spinous process	max	9.84	5.05	7.65	9.50	12.07
	min	3.02	4.50	4.42	2.64	5.20
	mean	6.69	4.77	5.59	5.32	9.94
	st. dev	2.08	0.19	1.14	1.52	3.23

1 17 in sample for width of caudal articular surface; 18 in sample for length of spinous process.

2 3 in sample for length including dens

SCAPULA

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		10	8	7	20	3
1 Proximal length	max	93.68	83.51	100.04	90.68	119.99
	min	82.94	73.37	75.25	67.03	104.51
	mean	86.91	79.17	89.91	78.62	111.92
	st.dev	2.98	3.87	8.11	5.53	7.76
2 Length of neck	max	19.60	17.00	20.28	19.57	28.46
	min	16.18	15.16	18.47	14.61	27.00
	mean	18.26	16.29	19.35	17.32	27.76
	st.dev	1.12	0.54	0.74	1.41	0.73
3 Height of neck	max	21.20	21.50	26.64	22.21	32.64
	min	18.20	18.20	20.40	16.72	26.91
	mean	19.82	20.15	23.82	19.77	29.28
	st.dev	0.91	1.08	1.87	1.33	2.99
4 Distal length	max	32.09	27.97	32.98	31.06	41.22
	min	29.25	22.52	28.79	26.16	38.03
	mean	30.54	26.91	30.70	28.80	40.00
	st.dev	1.02	1.81	1.51	1.52	1.72
5 Length of glenoid cavity	max	24.64	21.63	25.31	23.02	31.00
	min	21.61	20.22	20.39	19.57	29.63
	mean	22.95	21.05	23.36	21.49	30.48
	st.dev	0.93	0.43	1.81	0.95	0.74
6 Width of glenoid cavity	max	20.89	19.01	21.48	20.49	30.00
	min	18.38	17.01	18.84	17.44	26.55
	mean	19.66	18.09	20.43	19.08	28.43
	st.dev	0.82	0.63	1.02	0.99	1.75
7 Height of bone	max	145.00	141.80	162.50	147.50	184.20
	min	125.90	126.70	140.90	116.10	164.10
	mean	137.49	134.25	151.07	132.22	177.40
	st.dev	6.04	4.55	8.07	8.51	11.50

HUMERUS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8	20	4
1 Length of bone	max	139.80	133.52	148.10	142.59	200.70
	min	133.36	123.99	135.32	117.81	179.00
	mean	137.43	128.24	141.86	128.26	190.50
	st.dev	2.00	3.16	3.58	5.32	9.46
2 Proximal width	max	39.17	35.27	40.06	39.07	53.29
	min	36.72	32.35	35.79	29.51	47.10
	mean	37.72	33.46	38.28	33.69	50.88
	st.dev	0.89	1.07	1.58	2.10	2.77
3 Proximal depth	max	42.20	40.84	45.15	41.23	56.57
	min	38.00	32.88	35.77	33.20	51.84
	mean	40.30	36.25	41.38	36.76	54.11
	st.dev	1.41	2.26	2.99	1.98	2.29
4 Distal width	max	29.69	27.84	30.04	28.85	41.08
	min	27.34	25.13	26.90	23.06	36.79
	mean	28.62	26.27	28.13	25.91	38.82
	st.dev	0.76	0.81	1.23	1.26	2.12
5 Distal depth	max	25.86	22.57	25.39	23.79	31.44
	min	23.13	20.58	22.68	18.71	30.79
	mean	23.76	21.53	23.59	21.41	31.10
	st.dev	0.94	0.76	1.01	1.19	0.33
6 Min shaft width	max	14.83	13.97	15.30	14.45	22.94
	min	13.04	11.95	12.79	10.66	19.19
	mean	13.82	12.79	14.37	12.57	21.00
	st.dev	0.58	0.68	0.92	0.81	1.77
7 Height of coronoid	max	14.40	13.50	14.66	14.10	17.18
	min	13.23	12.31	12.85	11.32	16.17
	mean	13.85	12.75	13.61	12.71	16.57
	st.dev	0.45	0.38	0.68	0.71	0.45

RADIUS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8[1]	20[2]	4
1 Length of bone	max	147.40	143.80	162.10	155.00	201.50
	min	139.64	133.33	141.20	126.65	172.60
	mean	142.43	137.01	153.83	137.71	185.40
	st.dev	2.69	3.58	6.77	7.82	12.10
2 Proximal width	max	30.92	28.05	31.24	30.88	39.49
	min	28.29	26.43	27.46	25.96	37.76
	mean	29.71	27.31	29.80	27.81	38.92
	st.dev	1.15	0.55	1.10	1.77	0.81
3 Proximal depth	max	16.01	14.54	15.34	15.58	21.41
	min	13.55	13.08	13.96	12.83	19.95
	mean	14.88	13.90	14.65	14.06	20.53
	st.dev	0.74	0.48	0.98	0.77	0.63
4 Distal width	max	28.37	25.90	28.19	28.91	37.66
	min	27.20	24.63	24.50	21.84	35.49
	mean	27.64	25.29	26.66	25.32	36.38
	st.dev	0.41	0.42	1.14	2.15	1.03
5 Distal depth	max	19.87	18.77	21.16	19.47	28.60
	min	17.50	16.50	16.98	15.37	25.26
	mean	18.47	17.32	18.64	16.90	26.75
	st.dev	0.78	0.74	1.24	1.12	1.43
6 Minimum shaft width	max	16.47	15.18	17.33	18.82	25.14
	min	15.42	13.53	14.68	13.10	21.75
	mean	16.03	14.14	16.36	14.95	23.21
	st.dev	0.37	0.52	0.89	1.63	1.46

[1] 2 in sample for prox depth
[2] 19 in sample for prox width

ULNA

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8	20[1]	4[2]
1 Length of olecranon	max	40.55	37.50	44.70	43.09	58.28
	min	37.91	31.76	38.95	32.76	49.04
	mean	38.75	34.86	41.64	36.55	52.64
	st.dev	0.87	1.90	1.79	3.30	4.07
2 Depth of olecranon at beak of notch	max	26.54	24.40	28.30	27.39	34.03
	min	24.26	22.54	24.90	21.36	29.46
	mean	25.15	23.49	26.59	24.23	31.46
	st.dev	0.87	0.65	1.19	1.91	2.03
3 Width of proximal articular surface	max	21.14	17.40	19.47	21.67	28.42
	min	16.50	15.47	17.43	14.38	27.08
	mean	18.05	16.63	18.07	16.91	27.87
	st.dev	1.53	0.61	0.75	1.87	0.57
4 Depth of olecranon epiphysis	max	24.24	21.33	23.18	24.19	33.82
	min	21.40	18.20	18.98	17.98	27.87
	mean	22.18	20.19	21.03	20.32	30.05
	st.dev	1.00	1.08	1.54	1.75	3.28
5 Width of olecranon epiphysis	max	10.14	9.49	10.37	11.51	15.63
	min	8.83	7.94	9.28	7.95	14.62
	mean	9.63	8.87	9.75	8.95	15.12
	st.dev	0.52	0.57	0.35	0.84	0.51

[1] 19 in sample for depth of olecranon epiphysis
[2] 3 in sample for depth and width of olecranon epiphysis

INNOMINATE BONES

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7[1]	13[2]	7[3]	20[4]	3[5]
1 Length of bone	max	196.50	185.90	204.70	193.70	241.05
	min	171.60	167.10	161.90	161.40	197.10
	mean	185.69	175.95	184.50	179.40	225.14
	st.dev	8.58	4.72	12.60	10.20	20.39
2 Length of symphysis	max	53.97	51.81	54.55	55.70	75.78
	min	44.36	44.83	50.68	42.05	–
	mean	49.43	48.20	52.64	48.94	–
	st.dev	3.78	2.46	1.48	4.46	–
3 Greatest diameter of wing	max	78.98	75.52	76.60	71.34	88.16
	min	61.84	57.28	66.30	57.80	72.92
	mean	67.61	63.61	70.09	65.22	78.65
	st.dev	6.20	4.97	3.88	3.49	8.30
4 Length of ilium	max	104.90	102.10	111.07	107.33	141.02
	min	96.26	92.68	92.79	94.22	123.28
	mean	101.59	98.73	101.56	99.88	132.97
	st.dev	3.14	2.53	6.02	3.95	8.98
5 Length of acetabulum	max	27.96	24.68	27.98	27.87	34.78
	min	24.30	23.28	24.75	22.90	32.07
	mean	25.75	24.03	26.30	25.13	33.64
	st.dev	1.14	0.46	1.20	1.54	1.40
6 Depth of acetabulum	max	7.79	5.37	5.98	8.35	14.08
	min	4.82	2.12	4.50	2.41	12.32
	mean	6.35	3.32	5.12	4.77	13.29
	st.dev	1.07	0.86	0.49	2.00	0.89
7 Width of pelvis across acetabula	max	96.57	100.70	101.12	96.89	111.72
	min	93.03	88.59	95.78	86.35	–
	mean	95.02	93.87	97.75	92.42	–
	st.dev	1.47	3.31	2.16	2.79	–
8 Width of ischial tuberosity	max	102.74	112.76	129.56	108.29	96.60
	min	99.26	95.09	109.36	89.48	–
	mean	100.88	104.27	117.31	99.69	–
	st.dev	1.53	6.89	8.58	4.52	–

[1] 5 in sample for measurements 7 and 8
[2] 9 in sample for measurements 7 and 8
[3] 6 in sample for measurement 2; 5 for measurements 3, 7 and 8
[4] 18 in sample for measurements 7 and 8
[5] 1 in sample for measurements 2, 7 and 8; 4 for measurement 1

FEMUR

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8	20	5[1]
1 Length of bone	max	170.60	167.10	184.90	180.40	232.70
	min	161.60	151.90	165.10	150.70	177.10
	mean	166.78	157.62	174.65	159.63	202.70
	st.dev	2.93	4.94	6.96	7.18	27.50
2 Proximal width	max	45.37	40.70	47.17	47.46	58.77
	min	43.22	37.62	42.19	37.35	47.91
	mean	44.09	39.07	44.51	40.57	52.05
	st.dev	0.79	1.15	1.95	2.88	5.10
3 Depth of head of femur	max	20.09	18.51	19.58	20.08	25.76
	min	18.62	17.32	17.62	16.85	20.92
	mean	19.36	17.96	18.78	18.35	24.08
	st.dev	0.57	0.50	0.68	1.04	2.22
4 Distal width	max	37.90	33.92	37.35	38.71	46.17
	min	34.97	31.99	33.71	30.96	39.43
	mean	36.88	32.94	36.10	33.66	42.80
	st.dev	0.95	0.76	1.15	2.11	2.88

FEMUR (cont.)

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8	20	5[1]
5 Minimum width of shaft	max	15.17	14.45	17.71	17.36	22.48
	min	14.26	13.28	14.14	12.41	18.42
	mean	14.66	13.78	15.79	13.98	20.40
	st.dev	0.36	0.39	1.25	1.07	1.95

[1] 4 in sample for length of bone and proximal width

TIBIA

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		5	8	8[1]	20	4
1 Length of bone	max	199.40	194.45	219.20	214.40	263.90
	min	189.00	179.17	200.60	174.00	235.80
	mean	193.67	185.28	209.63	186.70	246.30
	st.dev	3.79	4.61	7.79	10.30	12.60
2 Proximal width	max	40.05	37.76	41.70	41.52	51.09
	min	38.72	34.74	38.69	33.41	48.66
	mean	39.42	36.19	40.13	36.63	49.62
	st.dev	0.62	0.94	1.00	2.09	1.18
3 Proximal depth	max	45.28	40.16	42.55	39.03	46.95
	min	38.50	34.20	37.50	31.22	40.69
	mean	41.74	38.44	40.08	34.52	44.19
	st.dev	2.86	2.05	1.62	2.43	2.76
4 Dorsal width	max	25.40	25.13	26.60	25.96	32.11
	min	24.14	22.30	24.20	21.20	30.44
	mean	24.75	23.59	24.86	23.01	31.33
	st.dev	0.51	1.02	0.85	1.20	0.78
5 Distal depth	max	20.53	19.16	20.98	20.16	23.02
	min	18.96	17.94	18.66	17.22	22.48
	mean	19.62	18.48	19.74	18.31	22.76
	st.dev	0.64	0.37	0.74	0.86	0.22
6 Minimum width of shaft	max	14.22	14.26	15.70	16.56	19.73
	min	13.33	12.25	13.80	12.07	17.81
	mean	13.84	12.80	14.86	13.23	18.57
	st.dev	0.35	0.63	0.75	1.07	0.83

[1] 7 in sample for length of bone, prox width and prox depth

PATELLA

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		5	4	7	19	4
1 Length of bone	max	29.73	26.96	30.23	28.83	39.60
	min	28.06	25.22	25.59	23.39	36.00
	mean	28.92	26.39	28.12	25.62	37.53
	st.dev	0.76	0.82	1.75	1.33	1.50
2 Proximal width	max	21.51	19.25	21.80	20.63	25.90
	min	18.77	17.24	19.12	16.66	22.94
	mean	20.40	18.25	20.52	18.52	24.98
	st.dev	1.03	0.84	1.01	1.08	1.37

TALUS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		9	8	7	20	3
1 Length of bone	max	28.67	25.87	28.20	30.53	34.13
	min	25.92	23.72	25.13	22.59	30.66
	mean	26.60	24.53	26.63	24.49	32.66
	st.dev	0.86	0.75	1.16	1.65	1.79

TALUS (cont.)

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
2 Distal width	max	18.24	17.11	18.28	19.94	21.94
	min	16.66	15.74	16.20	14.80	20.37
	mean	17.21	16.18	17.36	16.11	21.35
	st.dev	0.49	0.47	0.66	1.06	0.86

CALCANEUM

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	7	7	20[1]	4[2]
1 Length of bone	max	53.37	51.88	57.18	53.67	67.71
	min	51.34	47.90	52.68	45.09	64.42
	mean	52.22	49.91	54.57	49.72	66.27
	st.dev	0.68	1.60	1.92	2.19	1.68
2 Width of bone	max	19.89	18.60	20.42	19.91	25.05
	min	17.66	17.29	15.12	15.75	23.14
	mean	18.66	17.94	17.64	17.72	24.10
	st.dev	0.75	0.48	2.05	1.16	0.80
3 Length of central articular condyle	max	13.01	11.78	12.51	12.70	13.33
	min	10.76	10.47	9.25	10.10	12.86
	mean	11.82	11.20	10.45	11.37	13.12
	st.dev	0.69	0.53	1.31	0.60	0.19
4 Length of lateral process below condyle	max	9.90	9.70	11.65	10.30	13.96
	min	6.28	5.81	8.78	7.52	10.18
	mean	7.76	6.78	10.00	8.74	12.39
	st.dev	1.39	1.33	0.89	0.69	1.61

1 18 in sample for length of bone
2 3 in sample for length of bone

METACARPAL

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	8	8[1]	20	3
1 Length of bone	max	125.47	118.69	134.57	122.90	125.31
	min	113.52	113.16	118.90	102.82	116.34
	mean	119.93	116.15	127.54	114.18	121.32
	st.dev	4.44	2.30	5.07	5.34	4.57
2 Proximal width	max	22.77	21.19	22.99	22.39	29.83
	min	20.53	19.24	20.54	18.25	29.59
	mean	21.74	20.20	21.86	19.91	29.69
	st.dev	0.76	0.65	0.79	1.10	0.13
3 Proximal depth	max	16.71	19.16	17.06	16.85	19.96
	min	15.32	14.58	15.24	13.53	19.05
	mean	16.00	15.56	16.02	14.80	19.54
	st.dev	0.52	1.49	0.62	0.81	0.46
4 Distal width	max	25.12	22.96	25.22	23.70	33.41
	min	22.12	21.22	23.83	19.19	33.05
	mean	23.70	21.92	24.25	21.70	33.29
	st.dev	0.93	0.62	0.44	1.17	0.21
5 Distal depth	max	16.54	15.16	16.13	16.61	19.96
	min	14.94	14.39	14.43	13.36	18.68
	mean	15.71	14.78	15.37	14.64	19.38
	st.dev	0.49	0.31	0.65	0.92	0.65
6 Minimum shaft width	max	15.04	13.65	14.50	15.12	22.07
	min	13.35	11.88	12.86	11.50	21.82
	mean	14.10	12.59	13.79	12.82	21.95
	st.dev	0.63	0.66	0.56	1.01	0.13

METACARPAL (cont.)

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	8	8[1]	20	3
7 Depth of medial trochlear condyle	max	11.12	9.74	11.21	11.13	11.72
	min	9.72	9.32	9.72	9.11	11.33
	mean	10.54	9.67	10.43	10.04	11.53
	st. dev	0.46	0.14	0.58	0.52	0.20

[1] 7 in sample for depth of medial trochlear condyle

METATARSAL

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	8	8[1]	20	4
1 Length of bone	max	136.01	134.17	148.20	137.75	141.27
	min	122.77	123.15	132.08	112.26	128.18
	mean	128.66	126.59	140.58	124.47	133.05
	st.dev	4.54	3.75	5.73	6.49	6.16
2 Proximal width	max	20.10	18.62	20.43	19.40	24.07
	min	18.01	17.10	18.27	16.90	23.97
	mean	19.01	17.83	19.46	17.99	24.04
	st. dev	0.71	0.59	0.78	0.69	0.04
3 Proximal depth	max	20.39	18.81	20.89	20.05	24.06
	min	19.14	17.56	18.56	16.90	22.78
	mean	19.79	18.23	19.65	18.12	23.60
	st.dev	0.50	0.41	0.79	0.84	0.57
4 Distal width	max	24.05	21.86	24.02	23.45	31.29
	min	21.39	20.38	22.54	20.07	28.40
	mean	22.63	21.07	23.32	21.30	30.14
	st.dev	0.84	0.57	0.57	0.98	1.27
5 Distal depth	max	16.18	14.92	16.24	15.53	19.43
	min	14.63	13.98	14.31	13.61	18.23
	mean	15.42	14.53	15.37	14.43	18.63
	st.dev	0.48	0.33	0.69	0.54	0.54
6 Minimum width of shaft	max	12.77	11.77	12.79	13.33	17.77
	min	11.39	10.41	10.76	9.63	16.93
	mean	11.87	10.97	12.09	11.05	17.45
	st.dev	0.51	0.48	0.67	0.81	0.36
7 Depth of medial trochlear condyle	max	10.29	9.37	10.41	10.36	11.56
	min	9.00	8.74	9.10	8.60	10.81
	mean	9.65	9.13	9.79	9.33	11.14
	st.dev	0.43	0.21	0.60	0.49	0.32

[1] 7 in sample for depth of medial trochlear condyle

PHALANX 1

		FORE		HIND			FORE/HIND		
		Soay Male aged	Soay Female aged	Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	5	8	6	3	4	20	2
1 Length of bone	max	36.41	32.85	35.87	33.28	35.69	35.37	34.00	44.68
	min	32.26	31.34	33.59	31.44	33.84	33.99	29.45	43.14
	mean	34.74	32.01	34.30	32.24	34.93	34.66	31.43	43.91
	st.dev	1.37	0.75	0.72	0.69	0.97	0.68	1.11	1.09
2 Proximal width	max	12.76	11.28	11.74	11.74	12.34	12.72	11.66	15.01
	min	11.29	10.55	9.89	9.89	12.04	11.51	9.63	15.00
	mean	11.90	10.95	11.08	10.51	12.20	11.89	10.67	15.01
	st.dev	0.41	0.31	0.54	0.66	0.15	0.56	0.60	0.01
3 Proximal depth	max	15.54	13.58	14.54	13.69	14.19	14.47	14.25	17.14
	min	13.96	13.14	13.40	12.77	13.17	13.36	11.93	16.67
	mean	14.54	13.39	14.00	13.12	13.54	13.95	12.87	16.91
	st.dev	0.61	0.20	0.46	0.34	0.57	0.47	0.67	0.33

		FORE		HIND			FORE/HIND		
PHALANX 1 (cont.)		Soay Male aged	Soay Female aged	Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	5	8	6	3	4	20	2
4 Distal width	max	11.92	10.28	10.35	10.63	11.68	11.42	11.10	14.72
	min	10.36	10.02	9.06	8.78	10.56	10.12	8.79	14.16
	mean	11.05	10.14	9.90	9.23	11.28	10.82	9.75	14.44
	st.dev	0.56	0.10	0.45	0.70	0.63	0.56	0.65	0.40
5 Minimum shaft width	max	10.27	9.33	9.52	8.98	10.20	10.78	10.11	12.78
	min	9.25	8.42	8.06	7.86	9.35	9.19	7.39	12.49
	mean	9.77	8.83	8.69	8.36	9.79	9.79	8.61	12.64
	st.dev	0.40	0.40	0.47	0.45	0.43	0.73	0.68	0.21

PHALANX 2

		FORE		HIND			FORE/HIND		
		Soay Male aged	Soay Female aged	Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	5	9[1]	4	3	4	20	2
1 Length of bone	max	22.89	20.70	22.07	20.23	21.80	21.26	20.52	31.19
	min	19.96	18.94	20.14	18.86	20.51	18.64	16.73	30.93
	mean	21.62	19.68	21.14	19.45	20.97	19.97	18.54	31.06
	st.dev	0.95	0.78	0.69	0.60	0.72	1.08	1.02	0.18
2 Proximal width	max	11.95	10.45	11.00	9.52	11.39	11.98	11.12	13.97
	min	10.75	9.90	9.63	9.07	10.00	10.12	8.97	13.79
	mean	11.11	10.25	10.25	9.23	10.53	10.74	10.01	13.88
	st.dev	0.37	0.21	0.48	0.21	0.75	0.84	0.63	0.13
3 Proximal depth	max	13.04	11.93	11.61	10.91	12.51	12.26	12.51	15.20
	min	11.42	10.83	10.36	10.08	11.49	11.52	10.19	14.73
	mean	12.27	11.51	11.14	10.29	12.02	11.92	11.32	14.97
	st.dev	0.63	0.44	0.44	0.42	0.51	0.33	0.64	0.33
4 Distal width	max	10.54	8.89	8.88	8.06	9.25	10.20	9.07	12.12
	min	8.79	8.41	8.05	7.50	8.16	8.54	7.01	11.57
	mean	9.69	8.75	8.47	7.80	8.80	9.21	8.16	11.85
	st.dev	0.61	0.20	0.26	0.23	0.57	0.70	0.58	0.39

[1] 8 for prox depth

PHALANX 3—HOOF CORE

		FORE/HIND				
		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		9	7	6	20	2
1 Length of bone	max	27.16	26.77	29.84	27.12	34.61
	min	23.33	24.10	26.51	21.63	32.21
	mean	25.50	25.16	27.64	24.23	33.41
	st.dev	1.30	0.95	1.23	1.55	1.70
2 Height of bone	max	15.30	14.72	16.14	15.89	19.35
	min	13.05	13.99	14.67	12.46	18.06
	mean	14.59	14.34	15.40	14.22	18.71
	st.dev	0.82	0.25	0.58	0.93	0.91

Bull. Br. Mus. nat. Hist (Zool.) **56**(1): 57–61 Issued 31 May 1990

A new marine species of *Euplotes* (Ciliophora, Hypotrichida) from Antarctica

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SYNOPSIS. A new *Euplotes* morphospecies was isolated from marine sand sediments of Terra Nova Bay (Ross Sea, Antarctica), and grown in the laboratory. It belongs to the group of *Euplotes* species which are characterized by a dorsal silver-line system of the 'double' type and a set of 10 frontoventral cirri. A distinctive trait of the new species is a marked polymorphism, which develops in association with a food stimulus. The number of the dorsolateral kineties was found to be normally 10. However, most of the other diagnostic morphological traits showed conspicuous variations: i) the cell body dimensions varied from 38 × 30μm to 110 × 92μm, ii) the number of adoral ciliary membranelles from 45 to 65, iii) the number of silver-stained cortical alveoli aligned in the mid-dorsal interkinetal row from 12 to 18, and iv) the number of kinetosomes of the mid-dorsal kinety from 13 to 22.

INTRODUCTION

The marine Antarctic environment is populated by unexpectedly rich and diverse ciliate communities, which have been found inhabiting sea-ice slush of the lower layer of the pack, open water, sandy bottoms of coastal areas, and tidal pools (Hada, 1961, 1970; Fenchel & Lee, 1972; Thompson, 1972; Thompson & Croom, 1978; Buck & Garrison, 1983; Corliss & Snyder, 1986).

One of the most frequently encountered members of these communities appears to be *Euplotes*, a genus comprising numerous species with a wide geographical distribution and high adaptive potentialities (for a review: Curds, 1975).

Three different Antarctic marine species of *Euplotes* have so far been briefly described on the basis of light microscope observations. One was collected from Weddell Sea, recognized as new, and named *E. antarcticus* by Fenchel & Lee (1972). The other two, not identified, were collected from Palmer Archipelago (Thompson, 1972), and from South Shetland Islands (Thompson & Croom, 1978).

Here we describe, with the aid of the scanning electron microscope, a new Antarctic morphospecies of *Euplotes*, denominated *E. focardii*, three strains of which have been definitively established in our laboratory, where they are maintained under controlled conditions.

The relative ease with which *E. focardii* multiplies under controlled conditions producing large numbers of cells makes it attractive for the investigation of the genetical and biochemical mechanisms by which cell transformations are produced, as well as other relevant aspects of adaptation to the Antarctic environment.

MATERIALS AND METHODS

Sample collection and cell cultures

The sample of seawater and sandy sediment, from which *Euplotes focardii* was isolated, was collected (January, 1988) from a small cove, east of the Italian Antarctic base located at Terra Nova Bay (Ross Sea, 74° 42′ S, 164° 06′ E).

Collection was carried out by means of a 'Petersen' dredge hauled at a depth of 7 m. At the time of collection, the following environmental parameters were recorded: salinity, 35‰; temperature, −1.8° C; pH, 8.1–8.2. The sample was stored in the dark, at 2–4° C, for 3 months before being analyzed.

A dozen unknown *Euplotes*, later assigned to the new species *E. focardii* were individually isolated and supplied either with green algae *Dunaliella tertiolecta*, or unidentified bacteria present in the same antarctic sample and allowed to multiply following suspension with a Luria-Bertani medium (Bacto Tryptone 1%, yeast extract 0.5%).

Three *E. focardii* strains (labelled TN_1, TN_2, and TN_3) were definitively established, two starting from specimens fed with algae and one with bacteria. These strains are currently maintained in a cold room at 2–4° C under a rhythm of 16 h of darkness and 8 h of exposure to very weak light. Mating pair formation was observed neither in unmixed samples of the three strains, nor in their pairwise combinations. All the observations reported in this work were carried out on cells of strain TN_1.

Optical microscopy

Measurements of cell body dimensions refer to specimens fixed with glutaraldehyde vapour and were taken with a calibrated ocular micrometer mounted on an optical microscope. Silver-stained cells were prepared essentially according to Corliss (1953), except that fixation was carried out with 2.5% (v/v) glutaraldehyde in sea water for 60 min, at 4° C. Cells were also prepared according to the pyridinated silver carbonate method of Fernàndez-Galliano (1976).

Scanning electron microscopy

Cells for scanning electron microscopy were fixed for 30 min, at 4° C, using a modified Parducz solution, made by mixing six parts of 2% OsO_4 (w/v) in sea water (instead of in distilled water) and one part of saturated aqueous $HgCl_2$. Fixed cells were then (1) washed with 0.1 M cacodylate buffer, (2) mounted on cover-slip fragments previously treated with aqueous solution of 0.1% (w/v) L-polylysine, (3) dehydrated in a graded ethanol series, (4) quickly submerged in Freon 113, (5) critical point-dried in a Emscope CPD 750 apparatus, and (6) coated with gold in an Agar Aids sputter coater. Observations were performed with a Stereoscan 200 (Cambridge Instruments Ltd) scanning electron microscope.

Species registration

The holotype slide of silver-stained specimens of *E. focardii* is deposited at the British Museum (Natural History), London; accession number 1989:8:9:1. Cultures of *E. focardii* are available from our laboratory, and one living reference strain (TN_1) has been deposited at the Culture Collection of Algae and Protozoa, the Ferry House, Ambleside, Cumbria LA22 0LP, UK; strain number not yet assigned.

RESULTS

Diagnosis

Marine psammophilic species of *Euplotes* showing a dorsal argyrome of the 'double' type and a marked polymorphism that ensues in cultures suspended with plenty of food. The cirri are: 10 frontoventral, five transverse, and four caudal. Normally kineties (longitudinal rows of bristle cilia) are eight dorsal and two ventrolateral. Body shape may change from ellipsoid to roundish and body dimensions from 38 × 30μm to 110 × 92μm. The mid-dorsal kinety contains 13–22 kinetosomes and is flanked, on the left, by 12–18 polygons of the silver-line system. Adoral ciliary membranelles vary from 45 to 65. Nuclear apparatus consists of a large horseshoe-shaped macronucleus and one small, spherical micronucleus.

Etymology

The species denomination '*focardii*' (from Latin: of Focardi) was chosen in homage to Dr S. Focardi (University of Siena, Italy), who collected the sample of Antarctic water and sand from which *E. focardii* was isolated.

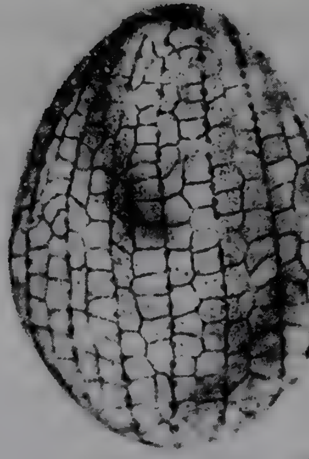
Associated ciliates

Other ciliates were found in association with *E. focardii*. They were identified as belonging to the following genera: *Aspidisca*, *Cyclidium*, *Diophrys*, *Epiclintes*, *Paraurostyla*, *Pleuronema*, *Uronema*, and *Uronychia*.

Morphology

The dorsal pattern of the *Euplotes focardii* argentophilic network (or 'argyrome'), that in silver-stained specimens reveals the juxtaposition of the cortical alveoli, is of 'double' type (Figs 1, 12), according to the designation of *Euplotes* argyrome types proposed by Gates & Curds (1979). Some disruptions of this regular pattern was occasionally observed in the largest specimens.

The number of argyrome polygons (cortical alveoli) that are longitudinally aligned on the left of the mid-dorsal (or central) kinety (identified as the sixth, counting clockwise from the post-oral kinety No. 1) varied from 12 to 18, in relation to the cell body size. On the cell ventral surface, the argentophilic network forms an unsystematic pattern, insignificant for species characterization.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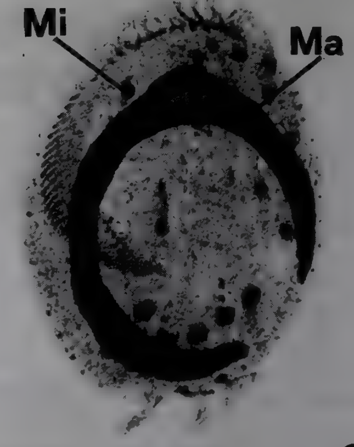

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Fig. 1 A silver-stained specimen showing the 'double' pattern of the dorsal argyrome. × 560.

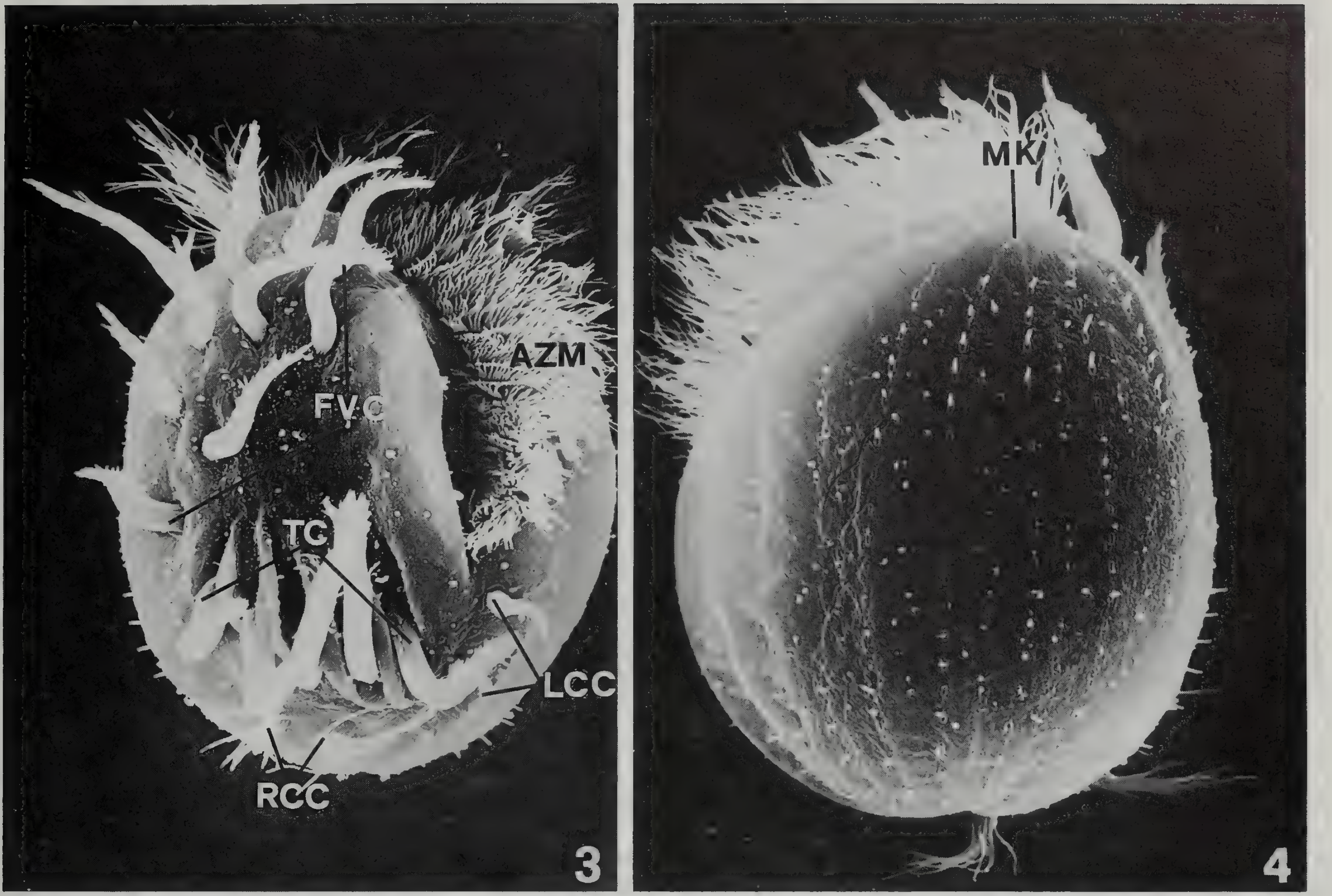
Fig. 2 A specimen in G_1 stage of the cell cycle, stained by Fernàndez–Galiano method, showing the macronucleus (Ma) and the micronucleus (Mi). × 560.

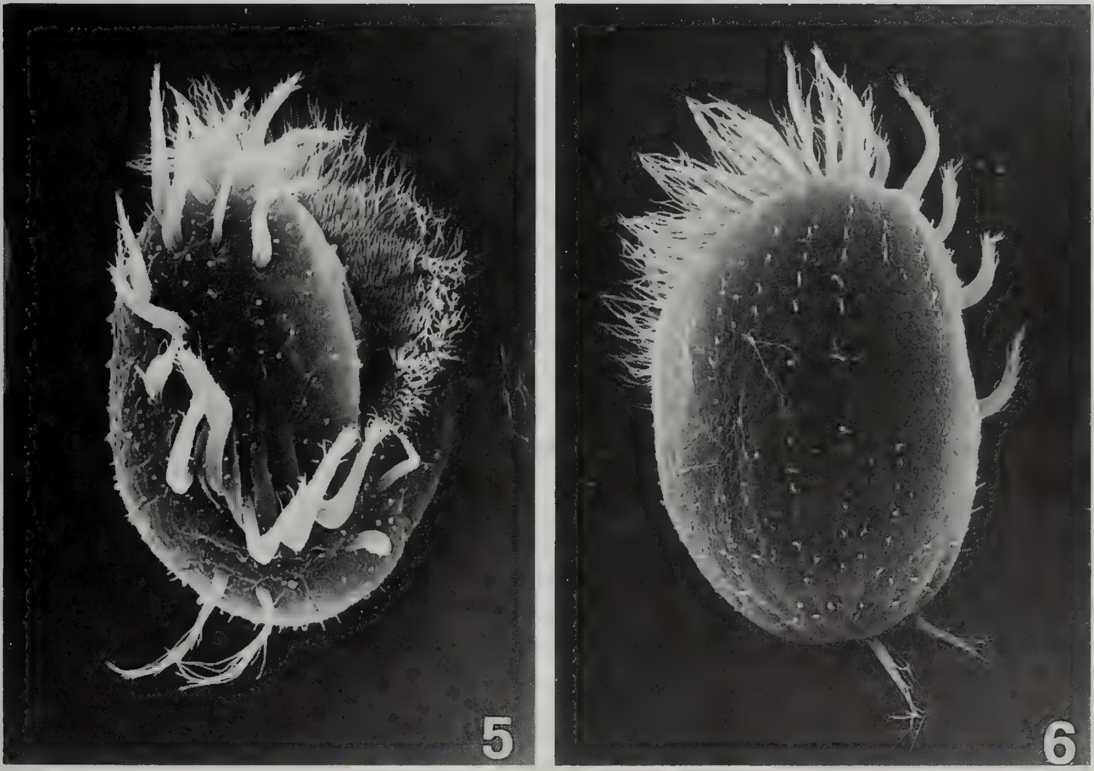
The nuclear apparatus (Fig. 2) consists of one macronucleus, which is horseshoe-shaped and usually huge, and one micronucleus, which is spherical, compact, and usually located close to the macronucleus in the upper left half of the cell.

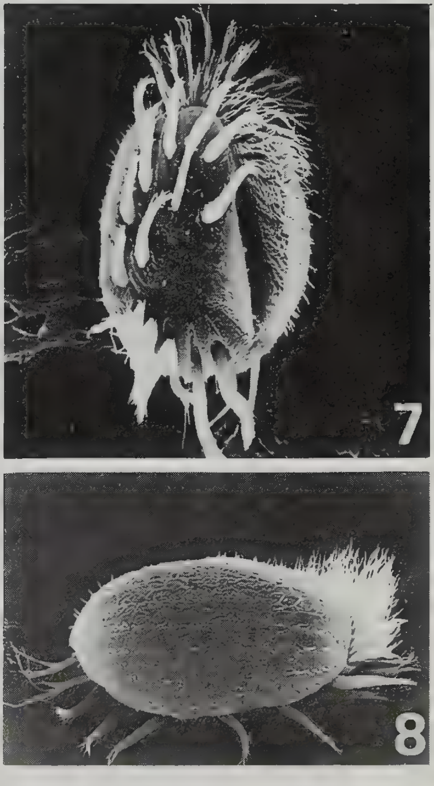
The contractile vacuole is usually visible in the largest living specimens and located immediately posterior to the insertion sites of those cirri which are conventionally named 'transverse' and labelled (according to Gates, 1977) 1/III and 1/IV.

Euplotes focardii dimensions and shape vary greatly in relation with the cell nutritive conditions, especially when green algae *Dunaliella tertiolecta* were used as food source. Voracious cells that reach 'giant' dimensions of 110 × 92μm regularly develop in cultures in exponential growth phase, when these are suspended with plenty of food (Figs 3, 4). These giant cells, sluggish in movement although very healthy and capable of dividing, usually represent 20–30% of the cell population rather uniformly characterized by average dimensions of 72 × 54μm (Figs 5, 6). Their fission rate is about twice as slow as that of normal cells, whose generation time is in the range of 2–3 days, and the giant feature of the parent cell persists in the two fission products. *Euplotes focardii* may sustain more than 3–4 weeks of starvation without an apparent decrease of viability. The only detectable effect of this prolonged starvation is a sharp reduction of cell body dimension to 40 × 30μm. (Figs 7, 8).

The overall body shape of *E. focardii* is ellipsoidal, with the left margin appreciably more convex than the right. However, cells replete with algae assume a nearly round shape and, in the giant cells, the left side of the body may swell conspicuously to form a transparent, triangular, wing-shaped protuberance. This swelling also demarcates a conspicuous widening of the oral area and of the surrounding adoral zone of membranelles. The anterior border usually appears more convex and shows a definite notch corresponding with the end of the adoral zone of ciliary membranelles. Both the dorsal and ventral surfaces appear poorly sculptured. On the dorsal



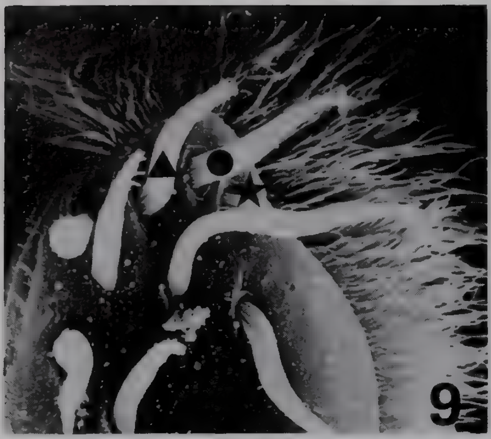


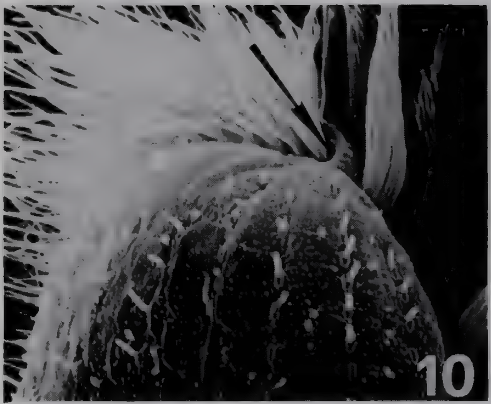


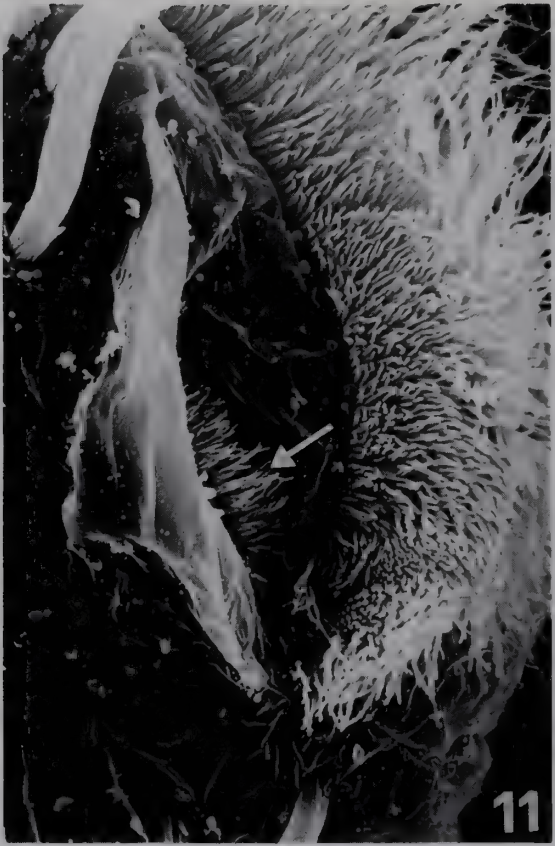
Figs 3, 4 Ventral and dorsal view, respectively, of 'giant' specimens isolated from a culture in exponential growth phase and showing the largest dimensions. AZM, adoral zone of membranelles; FVC, frontoventral cirri; LCC, left caudal cirri; MK, mid-dorsal kinety; RCC, right caudal cirri; TC, transverse cirri. × 680.

Figs 5, 6 Ventral and dorsal view, respectively, of morphogenetic stable specimens isolated from a culture at the beginning of the stationary phase, and showing 'standard' dimensions. × 680.

Figs 7, 8 Ventral and dorso-lateral view, respectively, of specimens isolated from a culture exposed to a prolonged starvation (3–4 weeks) and showing the smallest dimensions. × 680.







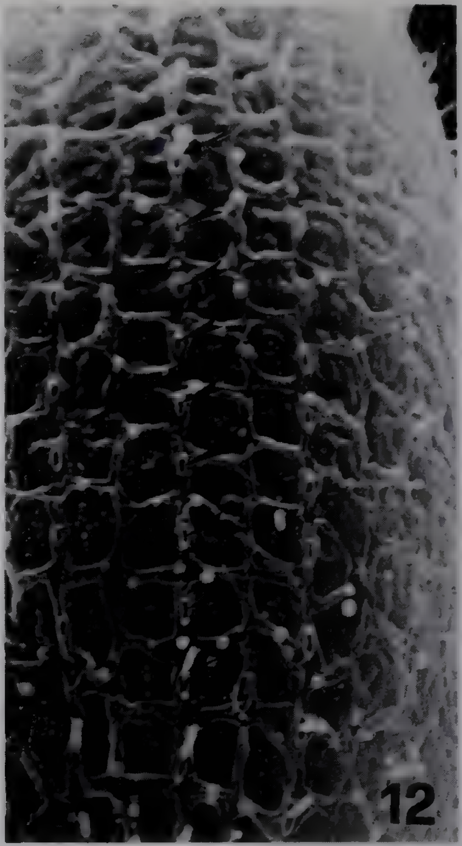


Fig. 9 Anterior region of the ventral cell surface showing the distinctive cone-shaped extremity on which are implanted three frontoventral cirri: 1/0 (star), 3/I (circle), and 3/II (triangle). × 1360.

Fig. 10 Anterior region of the dorsal cell surface showing the groove (indicated by an arrow) where are inserted the anteriormost adoral ciliary membranelles. × 2700.

Fig. 11 Overall view of the cytostomal area showing the well-developed paraoral membrane (indicated by an arrow). × 1700.

Fig. 12 Region of the dorsal cell surface showing, along the mid-dorsal kinety, pits with (arrows) and without (arrowheads) bristles. Also the 'double' pattern of the argyrome is visible. × 1630.

surface, only two ridges running over the left side are rather pronounced; six other ridges are inconspicuous and can be observed only in starved cells. The ventral surface bears four prominent ridges which run for only a short tract anteriorly from the set of five transverse cirri. Anteriorly it assumes a distinctive cone-shaped configuration (Fig. 9), which appears more pronounced in starved cells.

The oral area extends from about one-half of the body length in growing or early stationary-phase cells, up to three-quarters in very starved cells. It is delimited by an inner ribbed margin, which runs nearly straight for most its length. On the outer margin of the oral area are implanted 45–65 adoral membranelles composed of densely packed and unusually long cilia. The membranellar band extensively arches over the anterior border of the cell, where cilia are inserted on the bottom of a groove which deepens over the cone-shaped rostral extension of the ventral cell surface (Fig. 10). The cytostome opens in a rather recessed position and is fringed with a well-developed paraoral membrane (Fig. 11).

Euplotes focardii bears a complex of 19 cirri: 10 are frontoventral, five transverse, and four caudal. Three of the 10 frontoventral cirri—1/0 (or buccal cirrus), 3/I, and 3/II—are typically implanted on the cone-shaped rostral extension. Two of the four caudal cirri are inserted at the very rear of the cell right side and protrude considerably outside the body margin. The other two caudal cirri emerge from the left cell side, with the most anterior one typically positioned immediately below the bottom of the oral area. All cirri appear rather thick and fimbriate apically. This conformation of the cirral distal ends is consistent with the strong thigmotactic behaviour of *E. focardii*.

The bristle cilia align in 10 kineties (counted in samples of at least 100 specimens removed from cultures either in exponential growth, or in stationary phase), eight of which are dorsal and two latero-ventral. In giant specimens, one or two additional kineties, either complete or incomplete, were occasionally observed. It is worth noting that, as observed in scanning electron micrographs of other *Euplotes* species (e.g. Kloetzel, 1975; Ruffolo, 1976; Luporini & Dallai, 1980), cilia are missing in the equatorial and circumequatorial position of the cell, where only empty pits (and not ciliferous kinetosomes) are present.

The kinetosome number of each kinety remarkably varied in cells with different body dimensions. The kinetosomes of the mid-dorsal kinety varied from 13 in the smallest specimens to 22 in the largest.

DISCUSSION

In the genus *Euplotes*, three groups of morphospecies are conventionally distinguished (Gates & Curds, 1979) on the basis of the overall geometrical pattern of the dorsal argyrome—'single', 'double' or 'multiple'—according to the number of longitudinal rows of silver-stained polygons that align between any two adjacent kineties. The species of

Euplotes that we have designated as new, and denominated *E. focardii*, belongs to the group of 33 morphospecies with a dorsal argyrome of the 'double' type.

Within this group, 15 species bear 10 frontoventral cirri and 11 of them—*E. charon* (Müller, 1773), *E. balteatus* (Dujardin, 1841); *E. harpa* Stein, 1859; *E. alatus* Kahl, 1932; *E. trisulcatus* Kahl, 1932; *E. neapolitanus* Wichterman, 1964; *E. octocirratus* Agamaliev, 1967; *E. magnicirratus* Carter, 1972; *E. polycarinatus* Carter, 1972; *E. antarcticus* Fenchel & Lee, 1972; *E. rariseta* Curds, West & Dorahy, 1974—are marine sandwellers like *E. focardii*. Of the other four, three—*E. crenosus* Tuffrau, 1960; *E. inkistans* Tuffrau, 1960; *E. palustris* Ten Hagen, 1980—are inhabitants of fresh-water ponds, and one—*E. tuffraui* Berger, 1965—is endocommensal in the digestive tract of strongylocentroid sea urchins. Among the 11 marine morphospecies with a 'double type' argyrome and cirrotype-10, none shows the following array of structural traits which coexist in *E. focardii*: i) a basic number of 10 kineties; ii) variable numbers of adoral membranelles (45–65), of kinetosomes (13–22) in the mid-dorsal kinety, and of silver-stained polygons (12–18) on the left side of the mid-dorsal kinety; iii) a rostral cone-shaped extension of the cell ventral surface; iv) the leftmost caudal cirrus implanted immediately below the cytostome; v) a huge horseshoe-shaped macronucleus closely associated with a small spherical micronucleus.

This combination of morphological characters makes *E. focardii* clearly distinguishable from the two unidentified Antarctic species of *Euplotes* described by Thompson (1972), which unfortunately cannot be assigned to any group of *Euplotes* morphospecies because their descriptions lack any information on the type of dorsal argyrome.

On the other hand, the morphogenetic capability exhibited by *E. focardii*, in the presence of a persistent abundance of food, to develop giant individuals with an amplified oral area and excess of cortical organelles finds a striking counterpart in only one other marine species of *Euplotes*, *E. balteatus*. In cultures of *E. balteatus*, when the kind of food was experimentally changed from bacteria to small ciliates, Tuffrau (1964) observed the formation of unusally large individuals capable of ingesting more numerous prey. The occurrence of such extensive phenotypic polymorphism in *E. focardii* and *E. balteatus*, jointly with a large convergence of basic morphological traits, may argue for a close evolutionary relationship between these two species. Furthermore, in consideration of the fact that *E. balteatus* manifests a wide geographical distribution and a decidedly extraordinary capacity of exploiting different habitats (e.g., Kahl, 1932; Beers, 1954; Borror, 1963; Berger, 1965), we are led to speculate that *E. focardii* might have evolved by adaptive radiation from this species. Indeed, the capability to adopt different morphotypes in response to changes in the kind and amount of food might have greatly favoured an enhanced survival of individuals of *E. balteatus* spread into the Antarctic environment, where colonizing organisms must be endowed with special devices to cope with sharp seasonal variations in food resources.

Acknowledgements. Financial support was provided by the Italian National Program of Antarctic Researches (PRNA).

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Manuscript accepted for publication 12 October 1989

Bull. Br. Mus. nat. Hist (Zool.) **56**(1): 63–71 Issued 31 May 1990

Revision of the genus *Elzalia* Gerlach, 1957 (Nematoda: Xyalidae) including three new species from an oil producing zone in the Gulf of Mexico, with a discussion of the sibling species problem

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Synopsis. The marine nematode genus *Elzalia* is revised and three new species, *Elzalia poli*, *E. federici* and *E. kimae*, described from the oil producing zone of Campeche Sound in the Gulf of Mexico. *E. speculifer* (Timm, 1961) Hope & Murphy, 1972 and *E. tenuis* (Allgen, 1959) Gerlach & Riemann, 1973 are rejected as *spec. dub.* Pictorial & tabular keys to the genus are given. Some observations on the ecological and evolutionary significance of the genus are made.

INTRODUCTION

In 1986–88 samples of marine sediments were collected in the Campeche Sound, Gulf of Mexico, by the oceanographic vessel H–02 of the Mexican Navy, using Van Veen and Shipeck grabs. In 1986 eight samples were taken from near oil platforms in the Cayo Arcas region, the main loading point for oil tankers (Fig. 1, Table 1). More than 200 species of nematodes were extracted from the grey, jelly-like clay sediments in the samples, including three new species of *Elzalia*. This genus was absent in samples taken in 1987 from areas adjacent to the oil zone, but was present in samples collected from the Cayo Arcas region in 1988.

Table 1. Station localities (see Fig. 1)

Station	Latitude N	Longitude W	Depth (m)
1	21°00′	91°30′	37
2	20°30′	91°30′	30
3	20°20′	91°43′	37
4	20°11′	91°53′	42
5	20°07′	91°44′	37
6	20°00′	91°30′	31
7	19°45′	91°50′	53
8	19°25′	91°50′	42

This paper describes three new species of *Elzalia* from the Mexican samples. Pictorial and tabular keys to the genus are given, based on spicule and gubernaculum morphology. Some speculations on the zoogeography and the ecological and evolutionary significance of the genus are also made.

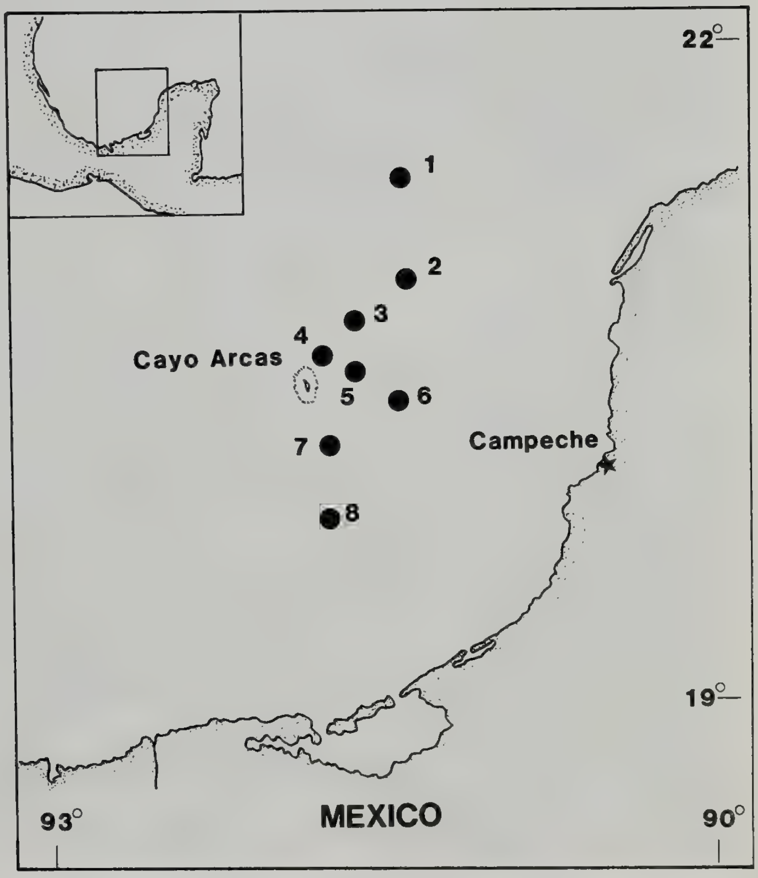


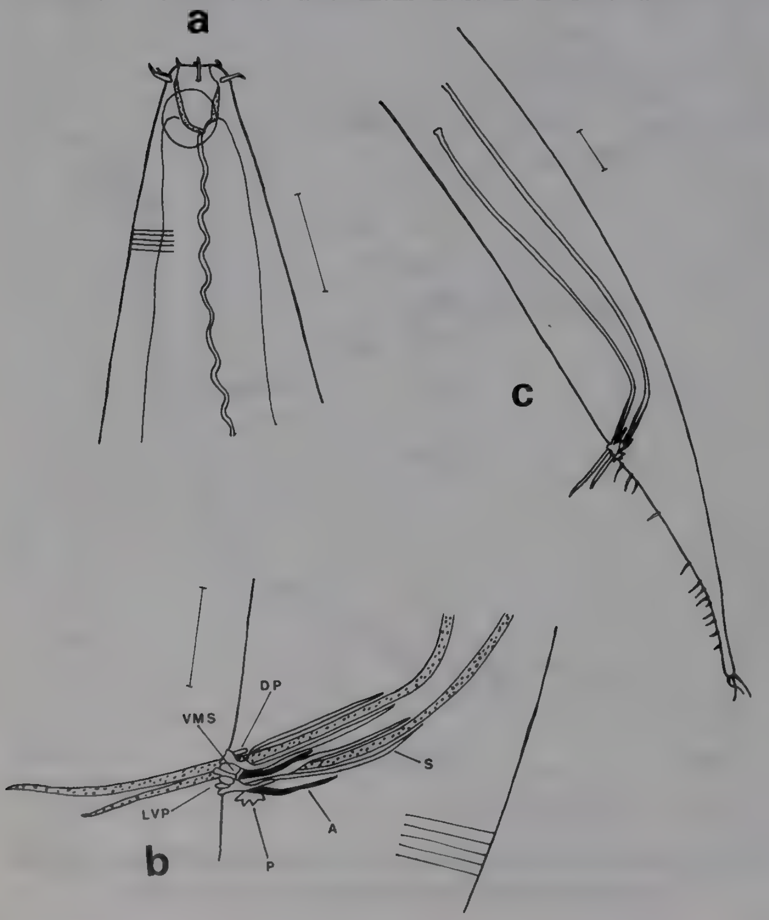
Fig. 1 Map of the Cayo Arcas region of the Gulf of Mexico showing sites from which *Elzalia* specimens were collected.

Table 2. Measurements of male specimens of *Elzalia poli*, *E. federici* and *E. kimae* (all measurements in µm unless otherwise indicated).

	E. poli				*E. federici*							*E. kimae*	
	Ep1	Ep2	Ep3	Ep4	Ef1	Ef2	Ef3	Ef4	Ef5	Ef6	Ef7	Ek1	Ek2
	Holotype		Paratypes		Holotype			Paratypes				Holotype	Paratype
Length (mm)	1.37	1.29	0.86	0.86	0.96	1.00	1.07	0.86	0.88	0.90	1.02	1.07	1.03
Head width	13	15	12	11	11	11	12	11	11	14	12	12	12
Maximum body width	86	83	47	43	56	56	50	28	56	50	58	64	58
Anal body width	55	56	35	33	27	39	42	25	39	40	39	36	43
Cephalic setae length	6	6	6	6	6	6	6	6	6	5	6	6	6
Amphid distance from anterior	6	6	3	3	3	3	3	3	3	6	3	3	3
Amphid width	11	10	8	8	10	6	11	6	8	9	10	7	7
Buccal cavity length	14	14	13	17	13	14	14	13	15	13	14	11	12
Buccal cavity width	8	9	8	6	6	6	6	6	8	8	8	8	9
Oesophagus length	283	200	175	167	200	192	200	167	175	167	208	167	175
Spicule length (arc)	300	333	128	150	124	242	235	117	133	107	133	75	69
Tail length	175	167	116	154	118	133	128	125	125	120	133	133	128
De Man ratios a	16	15	18	20	17	18	22	30	16	18	18	17	18
b	5	6	5	5	5	5	5	5	5	6	5	6	6
c	8	8	7	6	8	8	8	7	7	8	8	8	8

Table 3. Measurements of female specimens of *Elzalia* (all measurements in µm unless otherwise indicated).

	E1	E2	E3	E4	E5	E6	E7	E8	E9
Length (mm)	1.28	1.13	1.13	0.92	1.13	1.00	1.02	1.08	0.98
Head width	17	14	12	11	14	14	11	11	11
Maximum body width	78	56	58	55	72	69	53	53	42
Anal body width	42	28	31	31	42	36	28	28	28
Cephalic setae length	7	6	6	6	8	7	6	6	6
Amphid distance from anterior	3	4	3	4	5	4	4	4	6
Amphid width	12	8	12	8	8	9	8	10	9
Buccal cavity length	17	13	16	17	15	11	14	14	14
Buccal cavity width	8	8	7	6	9	8	4	6	6
Oesophagus length	208	200	200	167	208	208	208	208	183
Vulva distance from anterior	181	167	158	125	142	158	133	142	125
Tail length	633	592	558	492	583	517	533	558	450
De Man ratios a	17	20	19	17	16	14	19	20	24
b	6	6	6	6	5	5	5	5	5
c	7	7	7	7	8	6	8	8	8
V%	49	53	50	54	53	52	53	52	46



TAXONOMY

Generic diagnosis

Xyalidae. Spindle shaped colourless worms. No pigment spots or ocelli in preserved specimens. Cuticle finely, transversely striated. Buccal cavity prominent, cylindrical, cuticularized. Amphids large, circular or oval, granular in appearance, indistinct. Six labial papillae (R1), ten cephalic setae (R2 + R3). Somatic setae irregularly found, sometimes prominent ventral caudal setae, 3 distinct terminal setae. Oesophagus narrow anteriorly, widening posteriorly. Bulb absent. Spicules often long, slender. Gubernaculum often complex. Single anterior, outstretched testis, subventral right of intestine. Single anterior, outstretched ovary, lateral left of intestine. Tail conico-cylindrical, slightly clavate.

Remarks

Elzalia specimens showed few reliable specific characters, intraspecific morphometric variation seemed to be as large as

Fig. 2 *Elzalia poli*, holotype: (a) anterior, scale bar = 20µm; (b) gubernaculum and distal parts of spicules (black shading = dorsally directed apohpyses, stippling = spicules, see text for explanation of labels), scale bar = 20µm; (c) posterior showing spicules, scale bar = 30µm.

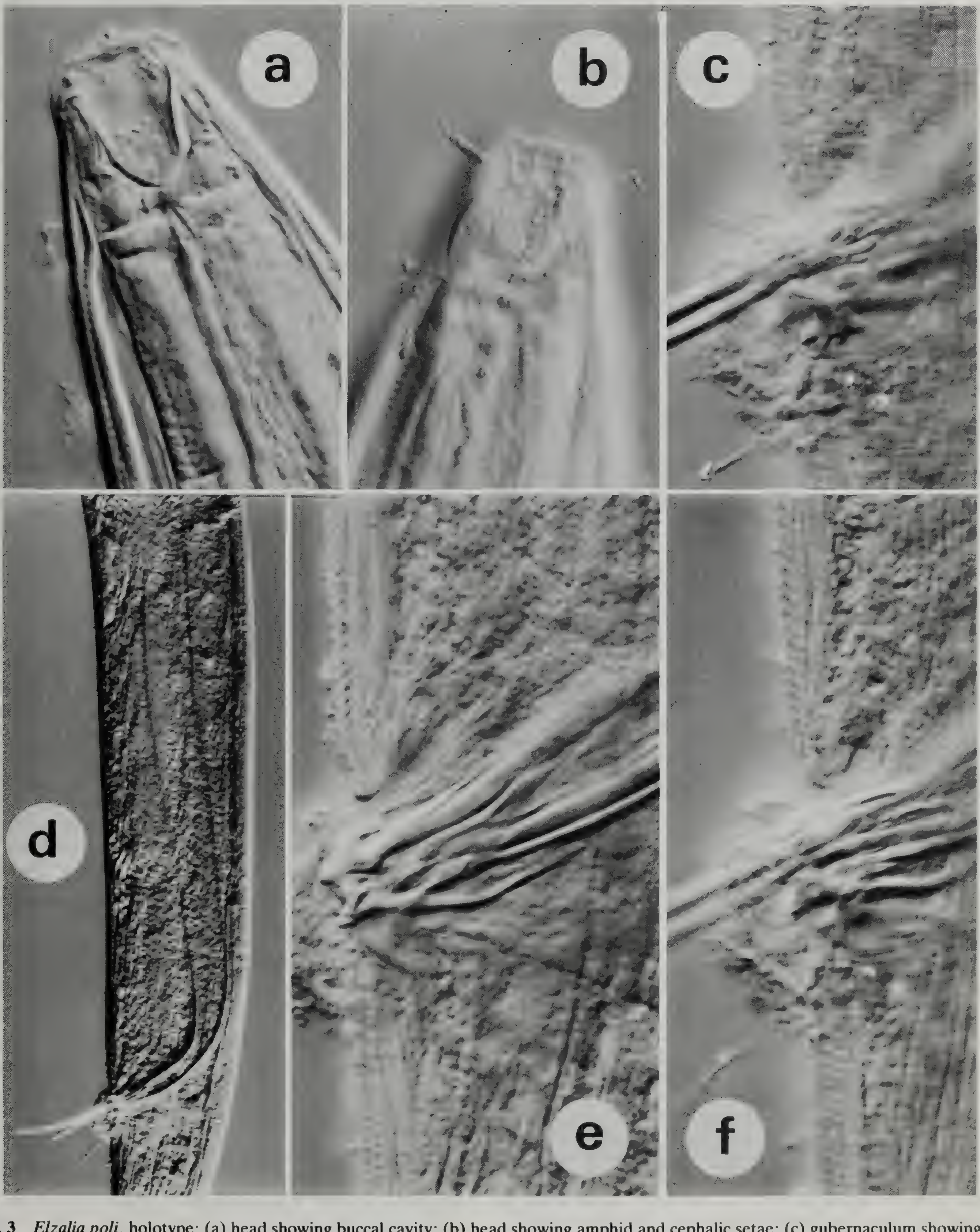


Fig. 3 *Elzalia poli*, holotype: (a) head showing buccal cavity; (b) head showing amphid and cephalic setae; (c) gubernaculum showing posteriorly directed 'leaf-like' projection; (d) spicules; (e) gubernaculum showing dorsal projections, spicule sheaths and dorsally directed apophyses; (f) same view as 'e', but at the focal plane of the spicules. 100 × objective used except 'd', 20 ×.

interspecific variation among males of the three new species. The possible exception was *E. mediterranea*, which was smaller than the other species. The body/spicule length ratio proved useful in distinguishing *E. kimae* (Table 4). The best character for distinguishing species proved to be spicule and gubernaculum morphology (see pictorial key, Fig. 9). The gubernaculum was often extremely complex and, although difficult to interpret, provided characters for specific diagnosis. No reliable characters to distinguish females and juveniles of different species were found.

Figure 6 of *E. kimae* shows a kink in the wall of the buccal cavity giving the appearance of a two chambered mouth. This was not a specific character as it appeared occasionally in some specimens of the other two species.

Lorenzen (1981) cited the position of the anterior gonad (to the left of the intestine) as the holapomorphic (synapomorphic) character which separates the Xyalidae within the Monhysteroidea. The location of the testis in *E. poli* and *E. federici* (and presumably other species in the genus) would seem to contradict Lorenzen's observation. Two other species were reported by Lorenzen to have anterior gonads on the right, *Hofmaenneria niddensis* and *Steineria pilosa*. The situation is further complicated in *Elzalia* because where the position of the ovary could be determined, it was on the left. Lorenzen (1979) reported that males and females of a species almost always show conformity in gonad position. He cited few exceptions (mostly involving species with one testis and two ovaries) none of which come from the Xyalidae. We hesitate to over-interpret this information because flattening meant that gonad position could be determined accurately in only a few specimens.

DESCRIPTIONS OF NEW SPECIES

The new species were described using male specimens. Females could not be determined and so are described *en bloc*.

Specimens were flattened by the mounting method so maximum widths are probably exaggerated and 'a' ratios underestimated. Measurements are given in Tables 2 & 3. Flattening also made it difficult to determine the lateral position of the gonads relative to the intestine.

Type material was deposited in the British Museum (Natural History).

Elzalia poli sp. nov.

(Figs 2 & 3)

Material studied. Holotype: Ep1, BM(NH) 1989.1.2. Paratypes: Ep2 & Ep3, BM(NH) 1989.1.3; Ep4, BM(NH) 1989.1.7. ('Ep' nos identify individual specimens, see Table 2). All males.

Locality: Ep1–3—Station 4; Ep4—Station 6. Specimens that were not used in this study were also found at Stations 1 and 2 (see Fig. 1).

Description. The morphological complexity of the gubernaculum gave rise to a distinct shape, albeit one with structures common to other members of the genus, which could be divided into four sections. The first was the ventral main section (VMS). This completely enclosed the spicules (with a possible anterior gap?) and was made up of a series of lateral and ventral projections (LVP) like the spikes on a mace, and a pair of dorsal projections (DP) anteriorly which gave the impression of two backward pointing hooks. The second section consisted of sheaths (S) extending along the spicules. Observations on a number of *Elzalia* males from different species suggested that the long thin spicules were protruded and withdrawn along these sheaths which act as 'guide rails'. The third section consisted of two slender, dorsally directed apophyses (A). The fourth was a pair of posteriorly directed 'leaf-like' projections or plates (P) which had four distinct triangular endpoints, two pointing posteriorly, one dorsally and one ventrally in most specimens (one had only 3 points). The spicules were long and slender. In one specimen (Ep4) the testis could be determined as subventral right of the intestine. Excretory pores and nerve rings were not observed.

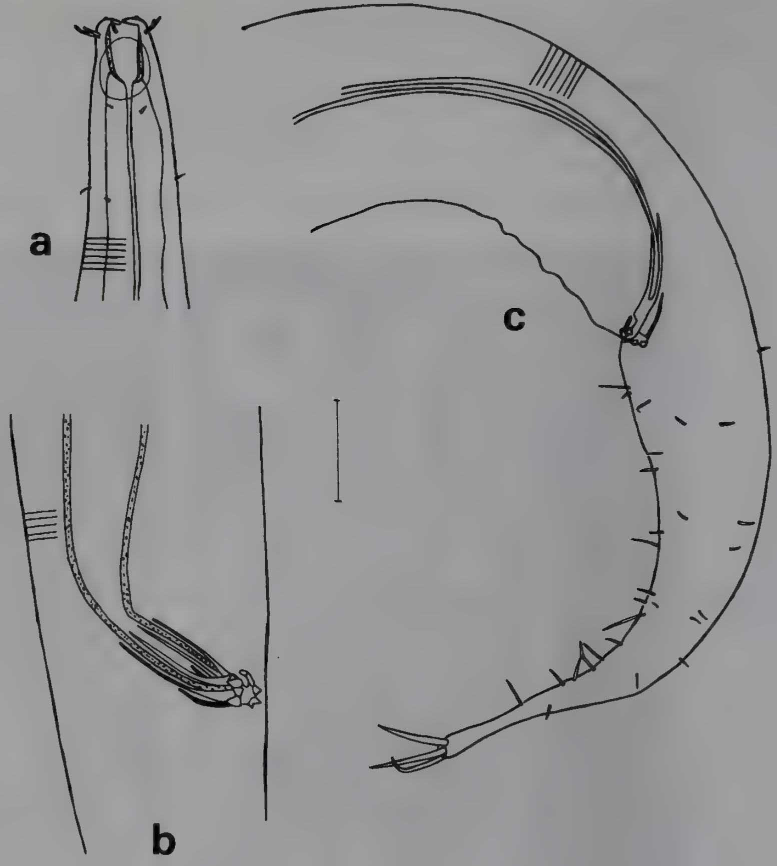


Fig. 4 *Elzalia federici*. Holotype: (a) anterior; (c) posterior (shading = dorsally directed apophysis). Paratype (Ef3): (b) gubernaculum with distal end towards observer, note 'finger-like' projections. Scale bar = 20µm.

Differential diagnosis. *Elzalia poli* sp. nov. could be distinguished from *E. mediterranea* Vitiello, 1971, by the simple gubernaculum and short body length (573µm) found in the Mediterranean species. *E. poli* is closely similar to the type species *E. floresi* Gerlach, 1957. The gubernaculum in *E. floresi* is simpler, with no lateral and only one ventral projection.

Remarks. Gerlach's specimen could be interpreted as having a gubernaculum essentially similar to the new species. It contained all four elements, in particular the four pointed posteriorly directed 'leaf-like' projections. The main section had one ventral projection and a structure that might be interpreted as an anterior 'hook'. The hypothesis that the new specimens were conspecific with *E. floresi* was considered and rejected because of (a) the simpler morphology of the latter's gubernaculum and (b) the large distance between the two localities (Southern Brasil and Mexico), which are separated by the Amazon estuary. However, further work along the

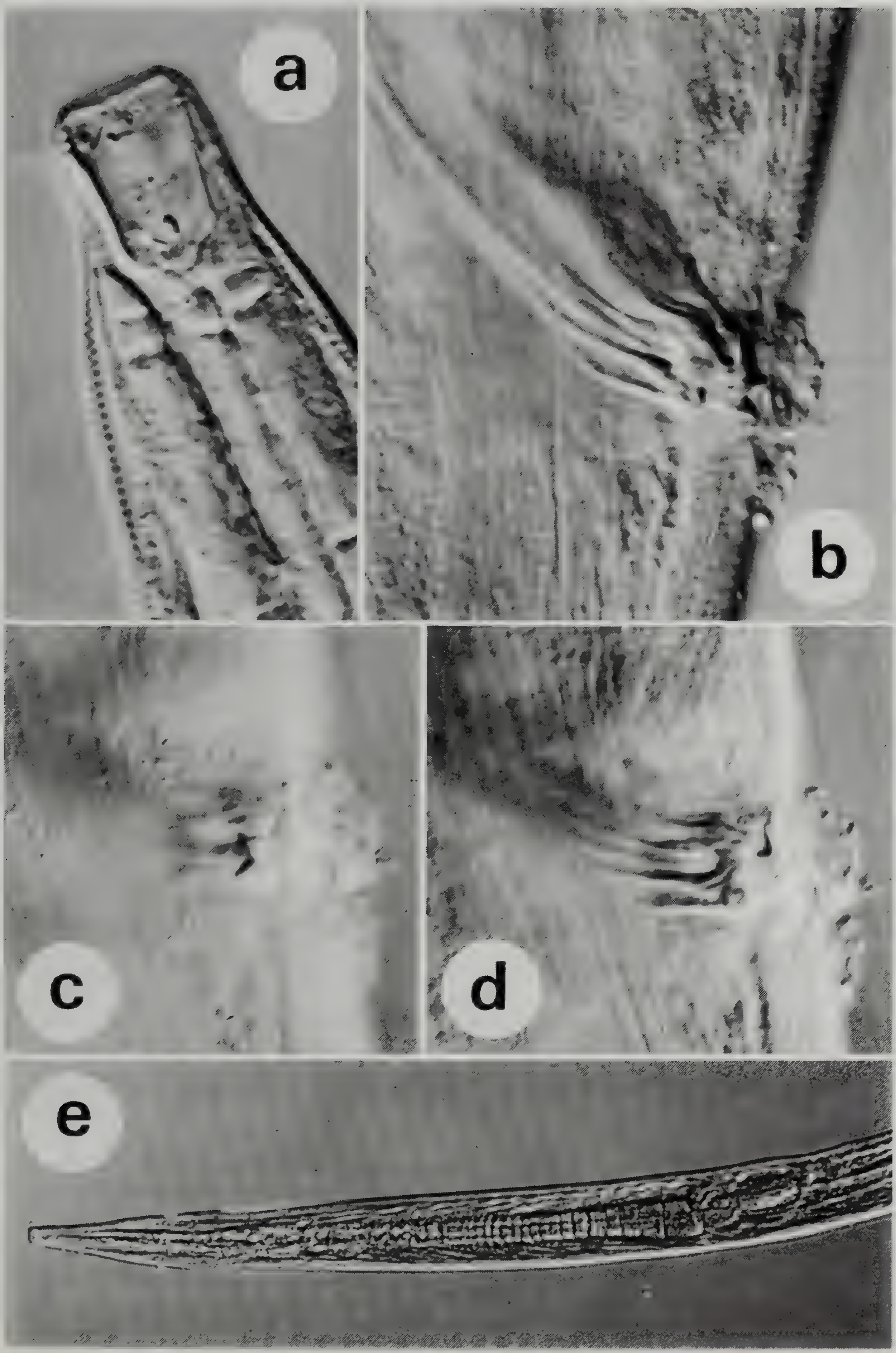


Fig. 5 *Elzalia federici*, paratype: (a) head showing buccal cavity; (b) gubernaculum (c.f. Fig. 4b); (c) distal end of gubernaculum showing 'finger-like' projections; (d) gubernaculum showing dorsal projection. *Elzalia* female (E3): (e) anterior showing ovary. 100 × objective used except 'e', 10 ×.

South American tropical coastline may indicate that intermediate forms exist in which case the two names might be synonymized.

Elzalia federici sp. nov.

(Figs 4 & 5)

MATERIAL STUDIED. Holotype: Ef1, BM(NH) 1989.1.6. Paratypes: Ef2, BM(NH) 1989.1.1; Ef3, BM(NH) 1989.1.4; Ef4, BM(NH) 1989.1.5; Ef5, BM(NH) 1989.1.8; Ef6, BM(NH) 1989.1.3; Ef7, BM(NH) 1989.1.9 ('Ef' nos identify individual specimens, see Table 2). All males.

LOCALITY. Ef1 & Ef8—Station 8; Ef2 & Ef6—Station 4; Ef3—Station 6; Ef4—Station 7; Ef5—Station 3. Specimens not used in this study were also found at Stations 1 and 2 (see Fig. 1).

DESCRIPTION. *Elzalia federici* was closely similar to *E. poli* except for gubernaculum shape. Principally, it lacked the posteriorly directed 'leaf-like' projections and the ventral main section was less complicated with finger-like projections on the left and right side of the distal part.

DIFFERENTIAL DIAGNOSIS. *Elzalia federici* sp. nov. is most similar to *E. poli* sp. nov. and *E. floresi* Gerlach, 1957 in size and general morphology but is distinguished by the absence of posteriorly directed 'leaf-like' projections on the gubernaculum. It can also be distinguished from *E. mediterranea* Vitiello, 1971 by the simpler gubernaculum and smaller body length described by Vitiello.

REMARKS. The close similarities between *E. federici* and *E. poli* and their presence in the same location suggested that they might be a single species exhibiting either (a) phenotypic variation or (b) apparent differences caused by functional morphology (eg. whether the spicules were protruded or retracted). However, no correlation was observed between gubernaculum appearance and any other factor (such as spicule position). Also the two shapes were always discrete, no intermediates were found. We, therefore, reject the hypothesis that they are conspecific. In a single specimen (Ef4) the single, anterior testis could be determined as subventral right of the intestine.

Elzalia kimae sp. nov.

(Figs 6 & 7)

MATERIAL STUDIED. Holotype: Ek1. Paratype: Ek2. BM(NH) 1989.1.4. ('Ek' nos identify individual specimens, see Table 2). Both males.

LOCALITY. Station 6 (see Fig. 1).

DESCRIPTION. The gubernaculum was simpler than the other new species described here but it showed the same basic morphology. The ventral main section lacked the spikes or finger-like projections described earlier and did not wrap around the spicules so completely but possessed a pair of posteriorly directed 'leaf-like' projections which ended in four posteriorly directed points. The sheaths extending along the spicules had thin dorso-ventral alae but spicules were shorter and stouter in this species. Lateral position relative to the gut of the single, anteriorly directed, ventral, testis could not be determined.

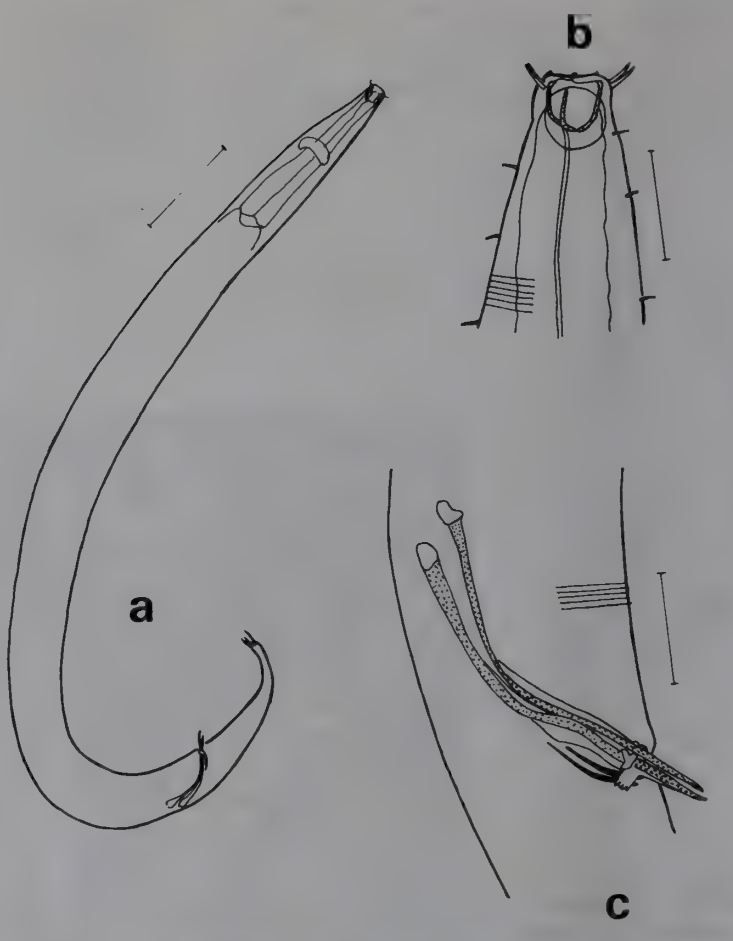


Fig. 6 *Elzalia kimae*, holotype: (a) whole animal, scale bar = 100μm; (b) anterior, scale bar = 20μm; (c) spicules and gubernaculum (shading as Fig. 2), scale bar = 20μm.

DIFFERENTIAL DIAGNOSIS. *Elzalia kimae* was distinguished from all other species of *Elzalia* by short stout spicules giving a high body length/spicule length ratio. *E. mediterranea* Vitiello, 1971, had a similar absolute spicule length to the new species but note that *E. mediterranea* was small so the body length relative to spicule length was low in this species (Table 4).

Female specimens

(Figs 7 & 8)

MATERIAL STUDIED. E1, BM(NH) 1989.1.5; E2, BM(NH) 1989.1.7; E3, BM(NH) 1989.1.10; E4, BM(NH) 1989.1.11; E5, BM(NH) 1989.1.12; E6, BM(NH) 1989.1.13; E7, BM(NH) 1989.1.14; E8, BM(NH) 1989.1.15; E9, BM(NH) 1989.1.16 ('E' nos identify individual specimens, see Table 3).

LOCALITY. E1 & E9—Station 7; E2, E3 & E5—Station 6; E4—Station 5; E6–8—Station 8 (see Fig. 1).

DESCRIPTION. Females were similar to the males of the three species in body characters. All had a single, anteriorly-directed, outstretched, ovary. In some specimens gonad position relative to the intestine could be reliably determined as lateral left. Sperm was occasionally observed in the variably sized post-uterine sac. Caudal glands were present and nerve rings were often observed.

Generic keys

Two tabular keys, one pictorial, to the valid species of the genus *Elzalia* are presented, Table 4 and Fig. 9.

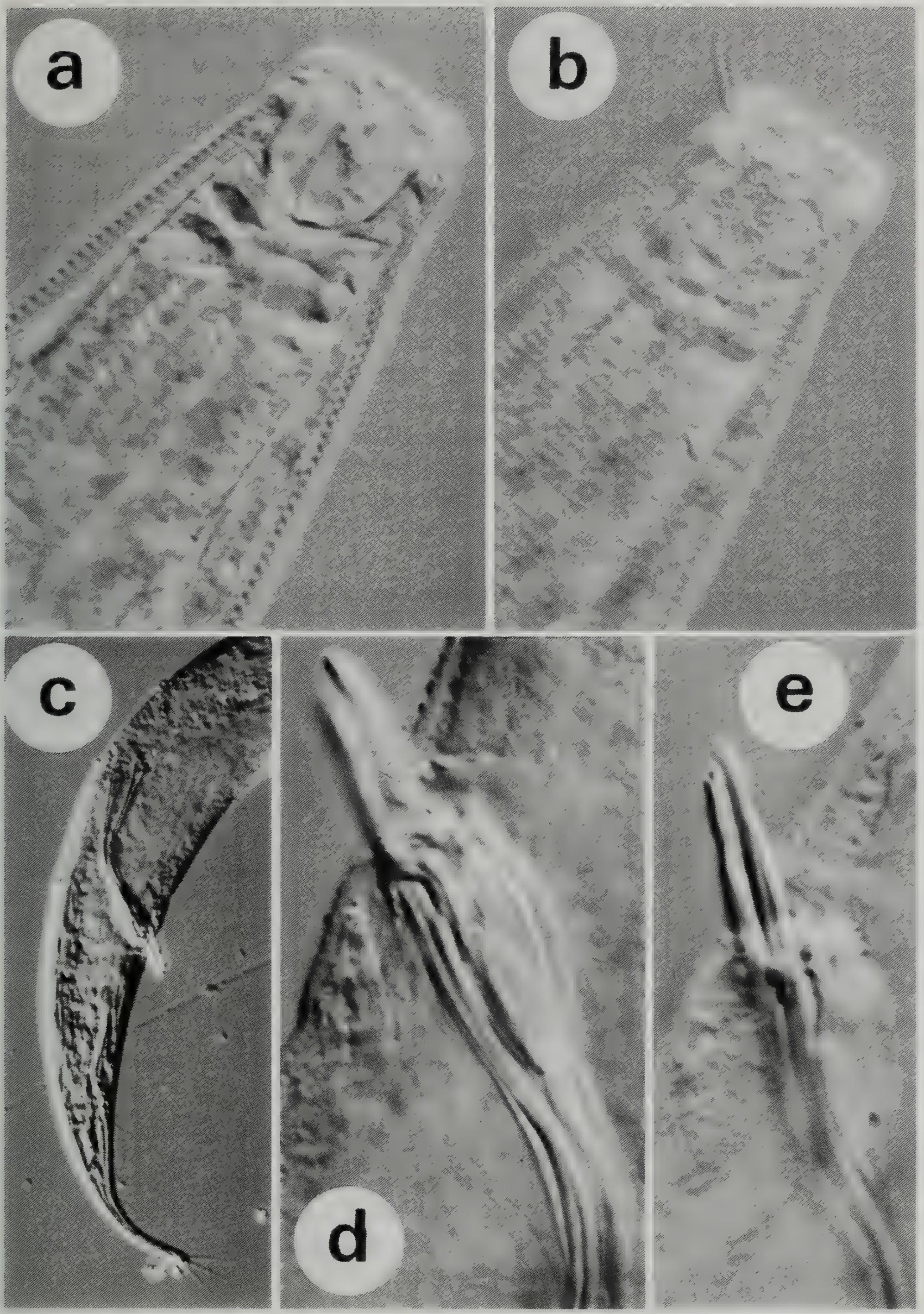


Fig. 7 *Elzalia kimae*, holotype: (a) head showing buccal cavity; (b) head showing amphid and cephalic setae; (c) posterior showing spicules and tail; (d) gubernaculum showing dorsal projections; (e) gubernaculum showing posteriorly directed 'leaf-like' projection. 100 × objective used except 'c', 20 ×.

Table 4. Tabular key to the species of the genus *Elzalia*

Species	length (mm)	Spicule arc length (mm)	length/spicule length ratio
E. federici	0.86–1.07	107–242	4.1– 8.4
E. floresi	1.04	170	6.1
E. kimae	1.03–1.07	69– 75	14.3–15
E. mediterranea	0.57	35	16.3
E. poli	0.86–1.37	128–333	3.9– 6.7

Gut contents

Diatoms were discovered in the guts of many specimens examined and in the intestine of a *Trichotheristus* specimen collected at the same time, together with a gubernaculum of *E. poli*.

Zoogeography

Elzalia was erected by Gerlach (1957) for *E. floresi* (type species) from the Sao Paulo region of the southern coast of Brasil. Vitiello (1971) described a new species from the Mediterranean, *E. mediterranea*. Hope & Murphy (1972) synonymised *Megalolaimus* Timm, 1961, transferring *M. speculifer* to *Elzalia*. Timm's description was of a solitary female but the current study (see below) suggests that only males can reliably be used to describe *Elzalia* species. It seems most unlikely that Timm's species could be recognised again with any certainty so it is here declared a *spec. dub*. However, the specimen was almost certainly *Elzalia* so the zoogeographic record of a member of this genus from the Bay of Bengal stands. Gerlach & Riemann (1973; see also Gerlach, 1963), transferred *Filipjeviella tenuis* Allgen, 1959, to *Elzalia*. This species was also described from a single female so is here considered *spec. dub*. But the description

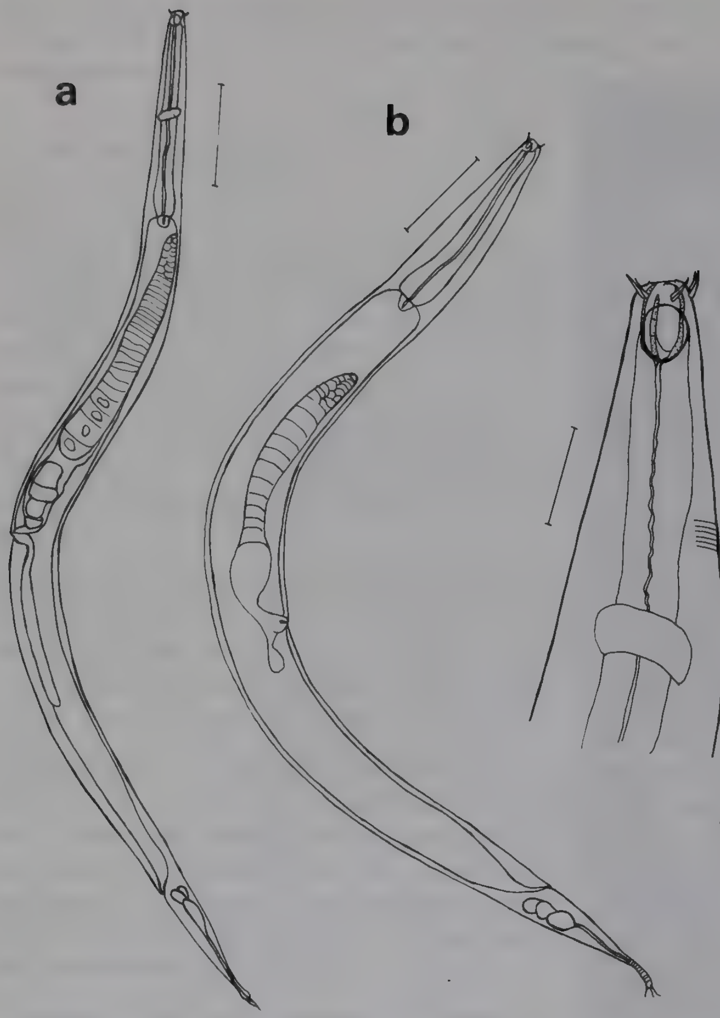


Fig. 8 *Elzalia* females: (a) whole body (EB), note large post-uterine sac, scale bar = 100µm; (b) whole body (E5), note small post-uterine sac, scale bar = 100µm; anterior (E4), scale bar = 20µm.

was weak and it is not certain to which genus the specimen belonged. For example, from the figure it appeared to have four cephalic setae. This specimen was collected from the Antarctic, unlike all other *Elzalia* records which are from warm waters (Bay of Bengal, Brasil, Gulf of Mexico, Mediterranean). This zoogeographic record should therefore be considered doubtful.

EVOLUTIONARY AND ECOLOGICAL IMPLICATIONS

The three new species described pose two questions. Of the five known *Elzalia* species why do we find three species so similar co-existing in the same area at the same time? Why do the males have such complicated cuticularized reproductive structures when the species are otherwise so similar that females are indistinguishable?

That large number of nematode species can be found apparently co-existing is a common observation (Platt & Warwick, 1980). Three or more species from one genus can apparently co-exist, eg. Lambshead (1986) surveyed a low-water spring tide, fine sand habitat at a specific time in the Clyde inland-sea area and found nine genera (out of 69, i.e. 13%) with three or more species present. Globally, nematodes exhibit enormous speciation, May (1988) estimates that nematodes and insects have in excess of one million species each. The figure of 4000 species of described marine nematodes (Platt & Warwick, 1980) is almost certainly a substantial underestimate because it is based mostly on studies in shallow temperate seas in the northern hemisphere. Deep-sea and tropical waters are richer in nematode species, most new to science (pers. obs.). This richness of nematode species is an anomaly for deterministic equilibrial ecology, particularly the co-existence of so many similar animals in, what appears to be, a homogeneous environment. This problem is usually explained in terms of resource partitioning by nematode species either by locomotion, or by morphological or physiological specialisation (Platt & Warwick, 1980).

Jensen, 1988, reported four *Acantholaimus* species co-existing in the Arctic deep sea. They had different buccal cavity morphologies which Jensen considered evidence of food resource partitioning. But such a situation is exceptional, *morphologically* similar co-existing species, as in *Elzalia*, represent the norm; hence Tietjen & Lee's (1977) speculation of *physiological* resource partitioning. In the Clyde survey (*op. cit.*) four species of *Neochromadora* were discovered, of which three were morphologically similar; while females and juveniles of the two *Leptolaimus* species were so similar that they could be distinguished only with great difficulty. If a non-deterministic, disturbance-controlled, or a deterministic chaos view of ecology is postulated then co-existence of similar species ceases to be an ecological problem but remains an evolutionary one. Assuming number of species is an indication of rate of speciation (Sanders & Grassle, 1971) then nematodes display high speciation rates. Jablonski & Lutz (1983) and Hansen (1978) found paleontological evidence that benthic invertebrate species with high dispersal rates (associated with pelagic larvae) have low extinction and speciation rates. Nematodes, which have conservative reproductive strategies, should have high extinction and speciation rates due to localization and vicariance events. This assumes that a conservative reproductive strategy is indicative of low dispersal rates. Such an assumption is reasonable but not necessarily true.

Closely related species co-existing, as in many marine nematode genera, implies effective reproductive barriers. Nematodes have complicated reproductive apparatus, especially in males. Such characters are important in a number of vertebrate and invertebrate taxa (Arnold, 1986). We may speculate on resemblances between nematode male reproductive structures and the 'key-lock' mechanisms found in taxa such as arthropods and lizards as a way of ensuring reproductive isolation between closely related, co-existing nematode species.

Finally, it is difficult to reconstruct phylogenies in a group with high rates of speciation and extinction due to both the loss of intermediate character states and high levels of homoplasy. Lorenzen (1981) produced a meticulously thorough phylogenetic reconstruction of the group. Nevertheless, even limited studies of warm water genera such as this revision of *Elzalia* produce exceptions to his cladogram and it is likely that further studies in tropical and deep-sea habitats will reveal greater problems.

Acknowledgements. We would like to thank Dr Luis Capurro, MC Gustavo de la Cruz and MC Gerado Gold of CINVESTAN, Biol Jean-Claude Fautsch of the Oceanographic Station of Campeche, and the Captain, Officers and Crew of the Mexican Navy Oceanographic Vessel 'H–02' for collecting samples, and to Gordon Paterson

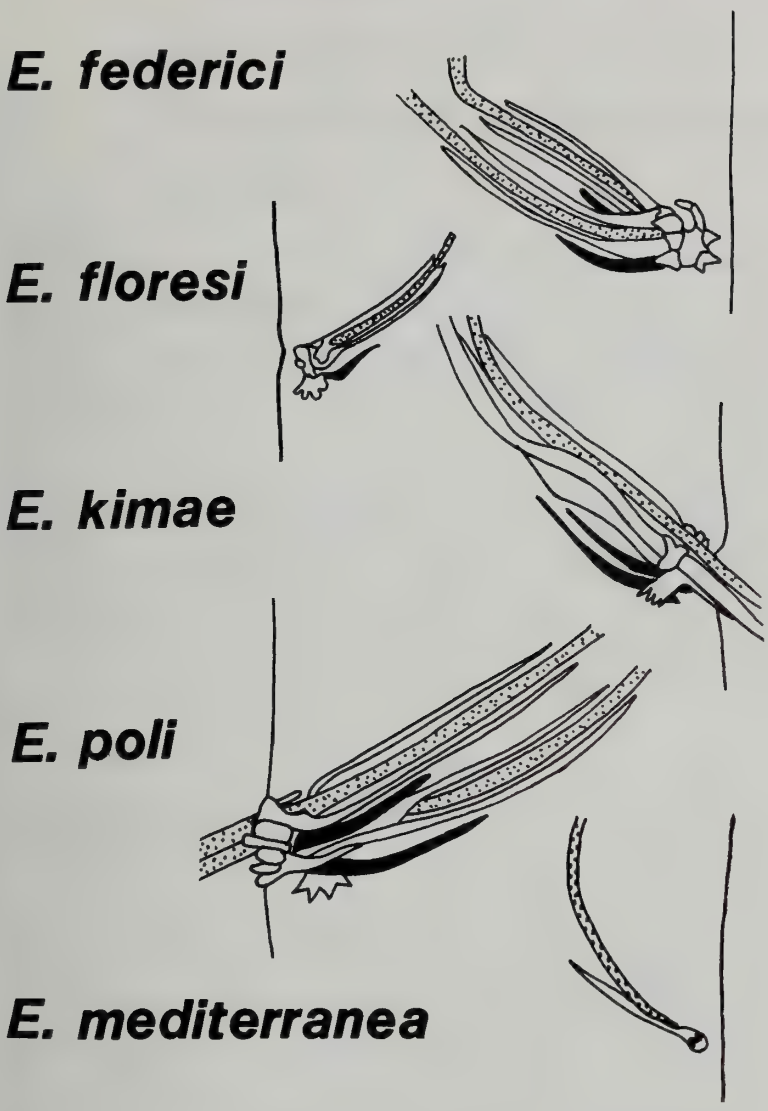


Fig. 9 Pictorial key to the genus *Elzalia* based on the morphology of the gubernaculum. All drawings are to scale (shading as Fig. 2).

and Howard Platt for advice and Martin Perry for assistance in preparing this work. Financial support for the project was provided by the British Council.

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Manuscript accepted for publication 3rd October 1989

Bull. Br. Mus. nat. Hist (Zool.) **56**(1): 73–91 Issued 31 May 1990

Records of *Nebalia* (Crustacea Leptostraca) from the Southern Hemisphere—a critical review

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Synopsis. The species concept '*Nebalia longicornis*' is composed of at least ten distinct species. Besides *N. longicornis* itself four of these were examined and are described in this paper as new species, viz. *Nebalia patagonica* (Magellan region), *N. antarctica* (Antarctic region), *N. falklandensis* (Falkland Islands), and *N. cannoni* (S. Georgia). Other specimens assigned to *N. longicornis*' could not be located and have not been described in sufficient detail to elucidate their true identity. This taxonomic confusion originates, in part, from Thiele's (1904, 1905) erroneous interpretation of *N. longicornis* Thomson, 1879 (which Thiele based upon a juvenile of *Sarsinebalia*) and also the excessively wide species concept previously applied to *Nebalia* species.

INTRODUCTION

The first species of *Nebalia* described from the Southern Hemisphere was *N. longicornis* G. M. Thomson (1879). The description was based upon a single mature male from Otago (Dunedin) Harbour on the East Coast of the South Island of New Zealand. Thomson, when describing this species, appears not to have had access to the paper by Claus (1879) in which sexual dimorphism of *Nebalia* was described. He therefore saw in the greatly elongated flagella of the antennae of this specimen a specific character and not an attribute of sexual maturity. This description of *N. longicornis* is too brief to permit an identification of the species. The drawing of the whole animal contains an error with respect to the articulation of the antennule. Only one feature of taxonomic value can be recognized, viz. the presence of only 1 spine on the anteriodorsal corner of the 4th article of the antennular peduncle. But as will be shown below, this feature is of very restricted value. Nothing is known about the fate of the type (Professor J. B. Jillett, personal communication).

Thiele, in two comprehensive reports on material collected by the German Deep Sea ('Valdivia') Expedition (Thiele 1904) and the German South Polar Expedition (Thiele 1905), produced the first major taxonomic contributions on Leptostraca from the Southern Hemisphere, including the description of the new genus *Nebaliella*. In both papers he also dealt with the genus *Nebalia*.

Claus (1887) previously had studied samples of *Nebalia* from widely different localities, but mainly from the Northern Hemisphere and had introduced a very wide species concept based upon a restricted number of morphological characters, viz. the shape of the compound eye, rostrum and the number of articles in the antennal flagellum. Thiele (l.c.) in dealing with his Southern samples of *Nebalia* accepted this species concept and referred all his specimens to *N. longicornis* Thomson (for details cf. section 3.2). Subsequent writers have followed Thiele, although Calman (1917, 1927) and Cannon (1931) expressed doubts concerning the validity of this taxonomic approach, and Johnson (1970) found its practical application unacceptable.

Dahl (1985) was able to show that Claus' species concept of *Nebalia* was too generalized and that the cosmopolitan *Nebalia bipes* of the western European coast is composed of a number of distinct species having distribution patterns similar to the other benthic invertebrates of this region.

The absence of authentic *N. longicornis* material has restricted progress on taxonomic studies of southern hemisphere Nebalids. In this paper arguments are examined which led Thiele to identify his material as *N. longicornis* (section 3). It also critically reviews, as far as has been possible, the synonomy of the southern hemisphere *Nebalia* species. The author has been fortunate in having had access to some of the most important collections previously referred to *N. longicornis* and a re-examination has led to the recognition of a number of new species described in section 5. In some instances, although lack of material or of adequate descriptions or drawings has made specific identification impossible, enough is known to state that these records refer to undescribed species. These cases are summarized in section 6, together with general conclusions.

THE REDISCOVERY OF NEBALIA LONGICORNIS THOMSON 1879

In 1985 Dr. G. C. B. Poore noted that the Sayce Collection in the Museum of Victoria contained a sample labelled 'N. longicornis', which he sent to me for study. These specimens are of particular interest because their tube contains two labels, one bearing the inscription 'cootypes' and the other stating that the sample was brought from New Zealand by G. M. Thomson, the author of *N. longicornis*.

The designation 'cootypes' cannot be correct, for Thomson (1879) stated explicitly that when making his description he had only the type at his disposal.

Unfortunately the labels in the tube give no information concerning the locality from where the specimens were collected. Taking into account the wide but generally accepted species concept introduced by Claus (1887) and the very incomplete original description given by Thomson (l.c.) this inevitably could cause doubt concerning the true identity of these specimens.

The type locality of *N. longicornis* is Otago Harbour, New Zealand. Prof. J. B. Jillett (pers. com.) has informed me that in this Harbour 'there appears to be only one *Nebalia* in the local shallow water habitats' and kindly sent to me three samples of *Nebalia* from several localities within that region. A critical comparison of an adult female from one of these samples with a similar example from the 'cootype' material reveals that they are conspecific and that this recent material unquestionably belongs to *N. longicornis*.

Although most material collected by Thomson came from Otago Harbour it is unfortunate that the true origin of the 'cootypes' is unknown. Therefore it is necessary to create a lectotype and paralectotypes for this species and these have been selected from the recent specimens sent to me by Prof. Jillett (see above and also Section 5).

THE INTERPRETATION OF *NEBALIA LONGICORNIS* BY THIELE 1904

The single specimen of *N. longicornis* having been lost and the description being too brief to permit identification, Thiele (1904) attempted to establish the identity of the only New Zealand specimen available to him of what he presumed to be a *Nebalia*, viz. a small specimen from Akaroa Bay near Christchurch on the East Coast of the South Island. Because this specimen was from New Zealand Thiele felt entitled to conclude 'mit ziemlich grossen Sicherheit' that it belonged to *N. longicornis*.

Thiele (l.c.) noted that this specimen lacked dark eye pigment and had a ventral subterminal rostral spine of which he made a drawing (l.c. pl.4, fig. 67). His concept of *N. longicornis* was influenced by a previous observation made on a sample of Leptostraca from Ireland, composed of small specimens with rostral spine and no dark eye pigment, a somewhat larger juvenile without rostral spine and with dark eye pigment, and an adult specimen of *Nebalia*. From this composite sample Thiele concluded that all the specimens in the sample belonged to *Nebalia* and that juveniles leaving the brood pouch lack dark eye pigment and retain a rostral spine that he presumed to be present in the embryo. This was to him a confirmation that the Akaroa Bay specimen was *N. longicornis*. Thiele had however, overlooked observations by Sars (1896) showing that the dark eye pigment in *N. bipes* begins to form in the brood pouch and that neither embryos nor juveniles possess a rostral spine. This was later confirmed by Manton (1934).

The specimen from Akaroa Bay is in the collections of the Zoological Museum of Copenhagen University. It was apparently damaged when collected and is generally in poor condition. I can however, confirm the absence of dark eye pigment. The eyes appear to be discshaped. There is no row of short 3-pronged spines on the margin of the exopod of the 1st pleopod as diagnostic of the genus *Nebalia* (Cf. SEM micrograph, Dahl 1985 fig. 115). The combination of disc-shaped eyes without dark pigment, a ventral subterminal rostral spine, and the absence of the spine-row mentioned above is diagnostic of the new genus *Sarsinebalia* (Dahl l.c.). The genus appears to be cosmopolitan and the type of the genus, *S. typhlops* (G.O. Sars 1896) occurs in Irish waters. The Irish sample seen by Thiele (l.c.) obviously contained specimens of both *Nebalia* and *Sarsinebalia*.

The small specimen from Akaroa Bay is not in good enough condition to serve as a basis for a descriptive account, but it is clearly a *Sarsinebalia*. With the exception of a specimen of *Nebaliella antarctica* Thiele (1904), also from the Akaroa Harbour, this was the only leptostracan recorded by Thiele (1904) from New Zealand. As will be shown in section 4 all other samples referred by Thiele (1904, 1905, 1907) to *N. longicornis* belong to other species. Only in one case is this conclusion based on indirect evidence.

It must be concluded, therefore, that Thiele (l.c.) never saw authentic specimens of *N. longicornis*, and his comprehensive discussions concerning the morphology and geographical distribution of this species and his comparisons with *N. bipes* are no longer valid and need not be taken into account.

RECORDS OF THE GENUS *NEBALIA* FROM THE SOUTHERN HEMISPHERE

Claus (1887)

Claus (1887) gave certain information concerning specimens of *Nebalia* from Chile in the Zoological Museum of the University of Vienna, collected by Schmarda. No mention was made of the exact locality. In an ovigerous female 11 mm in length Claus noted 16 articles in the flagellum of the antennule and 17 in that of the antenna. A smaller specimen showed a lower number of articles. The eye-stalk was strikingly long and the ommatidial part covered nearly the whole of it.

Thiele (1904), who had also seen these specimens but had not been permitted to dissect them, referred them, on account of the long rostrum and the armature of the antennule, to the 'Formenkreis der *N. bipes*'.

Claus (l.c.) who had studied specimens of *Nebalia* from different parts of the world concluded (l.c. p. 126) that the Arctic, Atlantic, Meditterranean and Adriatic populations, including what is now *Sarsinebalia typhlops*, belonged to one species which he called *N. serrata*, a name which, if valid, should rightly have been *N. bipes* (O. Fabricius 1780). In a footnote (l.c. p. 127) he named the Chilean form *N. chilensis* but stated that he could not decide whether it should be regarded as a 'Geographische Rasse' of *N. serrata* or as a separate species. Apart from the characters quoted above no description was given, and *N. chilensis*, although most probably referring to a new species, must remain a *nomen nudum*. No information on the specimens could be obtained from Vienna.

Claus (l.c.) also briefly discussed *N. longicornis*. Noting the lack of detail he concluded that his sample from Chile and *N. longicornis* should be regarded as belonging to 'dem engeren Typus aller von mir untersuchten Nebaliaformen'. This hardly implies more than that both belong to the genus *Nebalia*.

Thiele (1904, 1905, 1907)

Thiele accepted the views held by Claus concerning the extremely wide geographical range of *Nebalia* species and the considerable intraspecific variation. He regarded all specimens of *Nebalia* with a comparatively short and broad rostrum and a single spine on the 4th article of the antennular penduncle as belonging to *N. longicornis* and noted that it was difficult to find other good specific characters. As a result he reported *N. longicornis* from a number of widely separated localities, viz:

Pacific, New Britain, Blanche Bay (*N. longicornis*) (Thiele 1904) Pacific, Loyalty Islands, Lifu, Sandal Bay (*N. longicornis*) (Thiele 1904), Caribbean, Cuba (*N. longicornis soror* ssp. n.) (Thiele 1904), South America, Magellan Region, Ushuaia and Punta Arenas (*N. longicornis magellanica* ssp. n.) (Thiele 1904).

Antarctic, 'Gauss' Winter Station 1902–1903, 66°2′22″ S, 89°38′ E, 380–385 m (*N. longicornis magellanica*) (Thiele 1905).

This indicates a range of *N. longicornis* from tropical to sub-zero temperatures in the Antarctic and extending into most of the Southern Hemisphere.

According to Thiele (1904) the alleged *N. longicornis* specimens from New Britain and the Loyalty Islands were originally identified by Stebbing as belonging to *N. bipes*. They are not in the British Museum (Natural History) collections, and I have not been able to trace their whereabouts.

The drawing by Thiele (l.c. fig. 66) of the rostrum of a specimen from Blanche Bay, New Britain, is clearly different from that of the selected lectotype specimen of *N. longicornis*. He also figures the compound eye (l.c. fig. 69) without the well-developed eye papilla, clearly present in *N. longicornis*. Thiele's figures undoubtedly represent a new species, but in the absence of material it must remain undescribed.

The sample from Lifu in the Loyalty Islands is without documentation. Our present knowledge of the range of *Nebalia* species suggests that this tropical form is not identical with *N. longicornis* from the cool temperate waters of SE New Zealand.

The specimens from Cuba examined by Thiele (1904) had a comparatively long eye-stalk without a distinct eye papilla (l.c. fig. 77). This is certainly an undescribed species. The sample examined by Thiele belonged to the Zoological Museum, Berlin. The locality is outside the geographical range of the present study material, and I have not found it necessary to examine the specimens.

The new South-American subspecies *N. longicornis magellanicus* Thiele (1904) was probably based upon specimens from Punta Arenas on the Straits of Magellan collected by Ohlin (1896). Ohlin (1901) reports that he first identified this species as *N. longicornis*, but after comparisons with Arctic specimens of *N. bipes* he concluded that the two species were identical. Thiele (l.c.) based his identification of *N. longicornis* upon the presence of only 1 spine on the 4th article of the antennular peduncle and he regarded the well-developed eye papilla as diagnostic of the new subspecies *N. 1. magellanica* (l.c. fig. 68). Thiele (1905) mentioned further specimens from the Magellan region obtained by German collectors at Ushuaia and Punta Arenas in depths of 0–20 m, from which he confirmed the original observations on the compound eye.

The collections of the Swedish State Museum of Natural History examined by myself contain 7 samples of *Nebalia* from the Straits of Magellan and Tierra del Fuego, collected by various Swedish expeditions in the intertidal zone or in shallow water. All these samples contain only one species.

These specimens have the same armature on the antennule and the same characteristic eye papilla as drawn by Thiele for *N. 1. magellanica*. Moreover some samples, like those studied by Thiele, come from Punta Arenas and Ushuaia. They are undoubtedly conspecific with those described by Thiele as *N. 1. magellanica*. However, a comparison with the lectotype of *N. longicornis* reveals many differences and therefore *N. 1. magellanica* must be regarded as a new species. It is permissible to use the subspecific name '*magellanica*' for this new species, but unfortunately, as will be shown below, Thiele also referred another well-defined new species to *N. 1. magellanica*. To avoid unnecessary confusion the Magellan species is therefore named *N. patagonica* n.sp. and described in section 5.

In his report on the Leptostraca of the German South Polar Expedition Thiele (1905) recorded one sample from the 'Gauss' winter station at 66°22′2″ S, 89°38′E, 380–385 m. The sample consisted of 4 specimens, which he referred to the genus *Nebalia*. He noted, however, that the smallest specimen had the same type of rostrum with subterminal ventral spine and the same poorly developed compound eyes typical of his specimen from Akaroa Harbour, New Zealand. This specimen most probably represents another species of Sarsinebalia.

From one of the other three specimens, a large immature male, Thiele (l.c.) made drawings of the rostrum, compound eye, and 4th peduncular article of the antennule. Although aware of the fact that both the shape of rostrum and compound eye of his Antarctic specimens differed from those of his Magellanic material, he regarded the Antarctic ones as belonging to *N. 1. magellanica*. Later (Thiele 1907) in his report on the Leptostraca of the British National Antarctic Expedition recorded the occurrence of numerous specimens of *N. 1. magellanica* from a number of localities in the Ross Sea, and illustrated some of these. Calman (1917) found that a further specimen from the entrance of McMurdo Sound also agreed perfectly with the drawings made by Thiele. Having seen all the specimens from the Ross Sea and also a specimen from Commonwealth Bay, King George V Land, reported upon by Calman (1918), I share the view expressed by Calman (l.c.) that all these specimens from Antarctic coastal waters, including those from the 'Gauss' winter station, belong to the same species. This is also the case for the samples of *Nebalia* reported by Ledoyer (1969) from various shallow water localities off Adélie Land. The observations recorded by Ledoyer (l.c.) show that his specimens agree with descriptions and drawings made by Thiele (1905, 1907) of the specimens from Wilhelm II Land and Ross Sea and are therefore to be regarded as belonging to the same species. It is therefore now possible to conclude that hitherto only one *Nebalia* species, recorded from Wilhelm II Land, Adélie Land, King George V Land, and the Ross Sea, has been found in the coastal waters of the Antarctic continent.

However, comparisons of this large Antarctic species with *N. longicornis* and *N. patagonica* make it clear that it differs from both in many respects and that it must be designated as a new species. It is described in section 5 under the name *N. antarctica* n.sp.

Calman (1917, 1918)

As noted above, Calman (1917, 1918) contributed materially to the knowledge of *N. antarctica* n.sp., to be described below.

In addition, however, Calman (1917) in his report on the Leptostraca of the British Antarctic 'Terra Nova' Expedition 1910, recorded two specimens of Leptostraca, tow-netted off Northern New Zealand, one at st. 10, in the surface near Three Kings Island and the other at st. 15 in Spirits Bay.

Calman noted that both specimens were immature, one of them possessing a ventral subterminal rostral spine, 'regarded by Thiele as a juvenile character'. Calman provisionally referred both specimens to *N. longicornis*, at the same time however, expressing his doubts concerning the status of the species and the value of the presumed diagnostic characters. I have seen these two specimens which are in the collection of the British Museum (Natural History), but they are both juveniles and hardly suited to form the basis of a taxonomic description and I have refrained from dissecting them. The one with a small rostral spine is certainly a *Sarsinebalia*, the other one a *Nebalia*.

Cannon (1931)

Cannon (1931) reported upon the Leptostraca of the 'Discovery' collection. He dealt, in the first place, with *Nebaliopsis typica* G.O. Sars and *Nebaliella extrema* Thiele but also briefly with some samples of *Nebalia* and commented, like Calman (1917, 1927) upon the unsatisfactory status of *Nebalia* taxonomy.

I have been able to study this 'Discovery' material. It contains 4 samples of *Nebalia*, listed below together with the tentative identifications made by Cannon (l.c.) for three of them.

South Georgia, st. 45. 2.7 miles S. Jason Light. 6.IV.1926, 238–270 m, *N. longicornis magellanica*.
South Georgia, St. 144. 54°04′—53°58′ S, 36°27′—36°26′ W. 4.V.1926. 157–178 m Not mentioned by Cannon.
Falkland Islands, st. 51 off Eddystone Rock. 4.V.1926. *N. l. magellanica*.
South Africa, Simonstown, False Bay, Basin of H. M. Dockyard, 11.VIII.1926, 1–2 m. *N. longicornis*.

None of these specimens belong to *N. longicornis*. This is not surprising considering the vast distances separating the respective 'Discovery' stations from the type locality in New Zealand.

The two samples from S. Georgia both represent a new species, described in section 5 as *N. cannoni* n. sp. The single specimen from the Falkland Islands it also a new species, described in section 5 under the name *N. falklandensis n. sp.*

The specimen from Simonstown, S. Africa belongs to *N. capensis* K. H. Barnard (1914).

Other records

Reference has already been made above to the paper by Ledoyer (1969), which contributes information on *N. antarctica* n.sp.

Wakabara (1965) recorded and discussed a species of *Nebalia* collected in Brazil at Ubatuta, 23°57′S, 45°06′W. His drawings show considerable individual variation of the spinous armature of the 4th article of the antennular peduncle in his 6 male and female specimens. A reference to the lack of denticlation is difficult to understand. If it refers to pleopods 3 and 4 it is worth noting. This is undoubtedly a new species which should be given a complete description.

Johnson (1970) reported the presence of a population of *Nebalia* at Singapore. He discussed critically the specific criteria applied by Claus (1887) and Thiele (1904, 1905, 1907) and, finding them unsatisfactory, did not specifically identify his specimens.

From Southern Africa two valid species have been described, viz. *N. capensis* K. H. Barnard (1914) from Cape Town (cf. above) and *N. ilheoensis* Kensley (1976) from S. W. Africa.

Finally Dahl (1985) reported *N. strausi* Risso from St. Helena. The species is also known from Madeira, the Western Mediterranean and the West Coast of Europe to NW France and the Channel Islands.

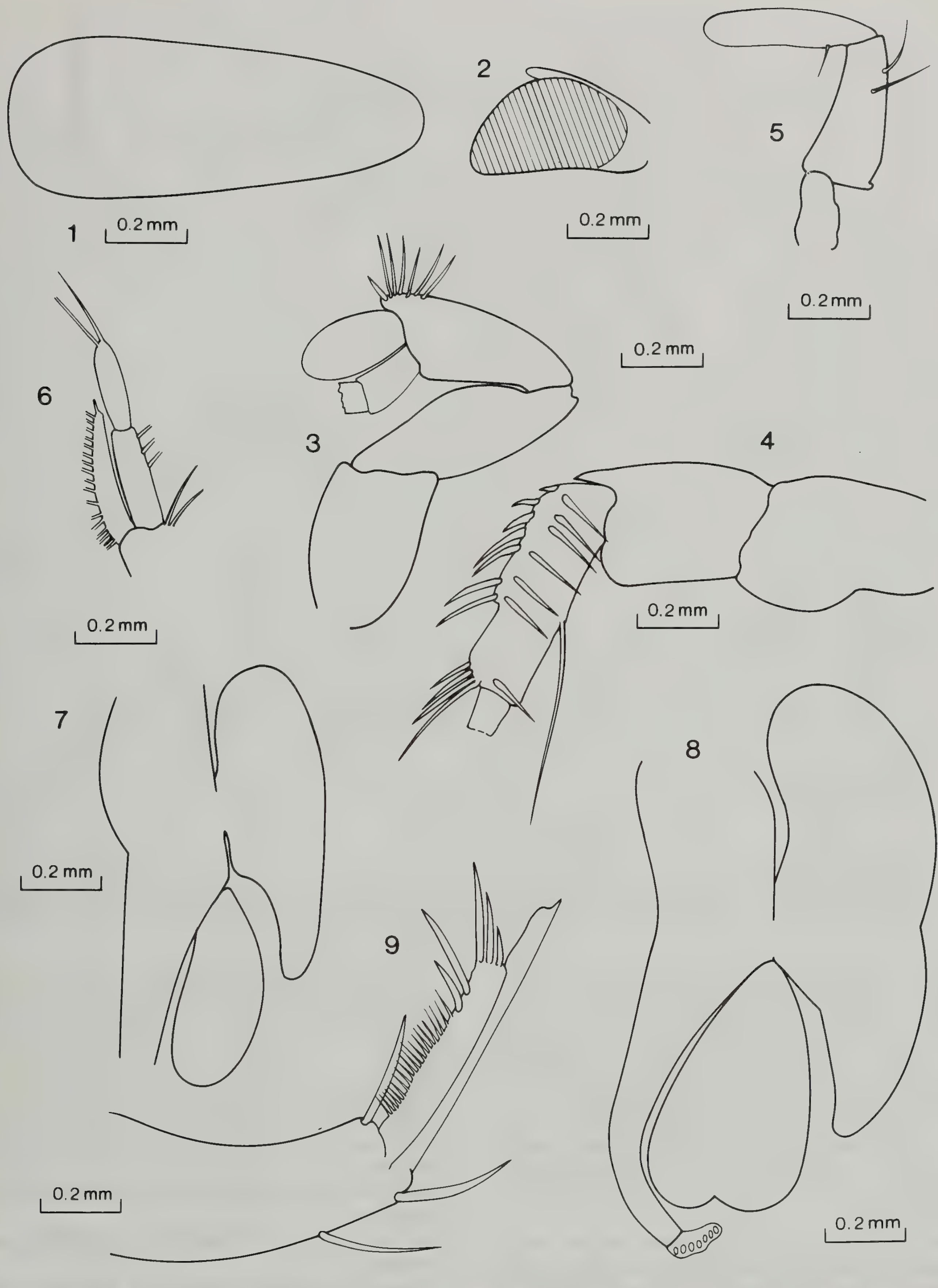
DESCRIPTIONS

Nebalia longicornis Thomson (1879).

Description of female lectotype.

TYPE LOCALITY: New Zealand, South Island, Otago Harbour, Portobello Mar. Biol. Stat. Locality 14 B 12_2, 18 fathoms. July 7, 1965. 2 paralectotypes.

Status of female: Postovigerous.
Carapace length: 2.7 mm.
Rostrum: long and narrow (fig. 1), 2.6 times as long as wide, slightly broader near base, tapering very gradually to comparatively narrow, rounded point.
Pleon, telson, furca: 4th pleon epimeron(fig. 10) with posterolateral corner produced to form acute point, posterior margin with comparatively long, rounded denticles, becoming gradually somewhat broader proximally. Crenulation on dorsum of pleon segments 6 and 7 (fig. 14) with denticles rather long, distally rounded and not very closely packed. Anal scales (fig. 15) with medial margin slightly convex, point long and acute over medial part of scale, lateral margin very slightly concave, sloping evenly and lacking 'shoulder'. Furcal rami (fig. 16) shorter than combined length of telson and 7th pleon segment, only proximal part of medial margin with setae between lateral spines, lateral margin only with dense row of spines.
Compound eye: (Fig. 2) with well developed eye papilla produced over dorsum of eye, ommatidial part covering most of the eye-stalk. Supraorbital plate over both compound eyes damaged.
Antennule: (fig. 3) with 2nd article of penduncle somewhat longer than 3rd article; 4th article with only one spine on distal corner and 6 setae along dorsal margin. Antennular scale elliptic, 2 times as long as wide. Flagellum of both antennules broken near base.
Antenna: (fig. 4) with penduncular articles comparatively short; 3rd article only slightly longer than 2nd article, on right antenna with lateral spine-row composed of 8 spines plus one distal spine, on left antenna only 6 spines, some possibly lost.
Mandibular palp: (fig. 5) with 2nd and 3rd articles subequal in length; 2nd article with one small tubercle on proximal corner and one marginal and one lateral seta on distal part, both rather short; 3rd article straight, only expanding very slightly



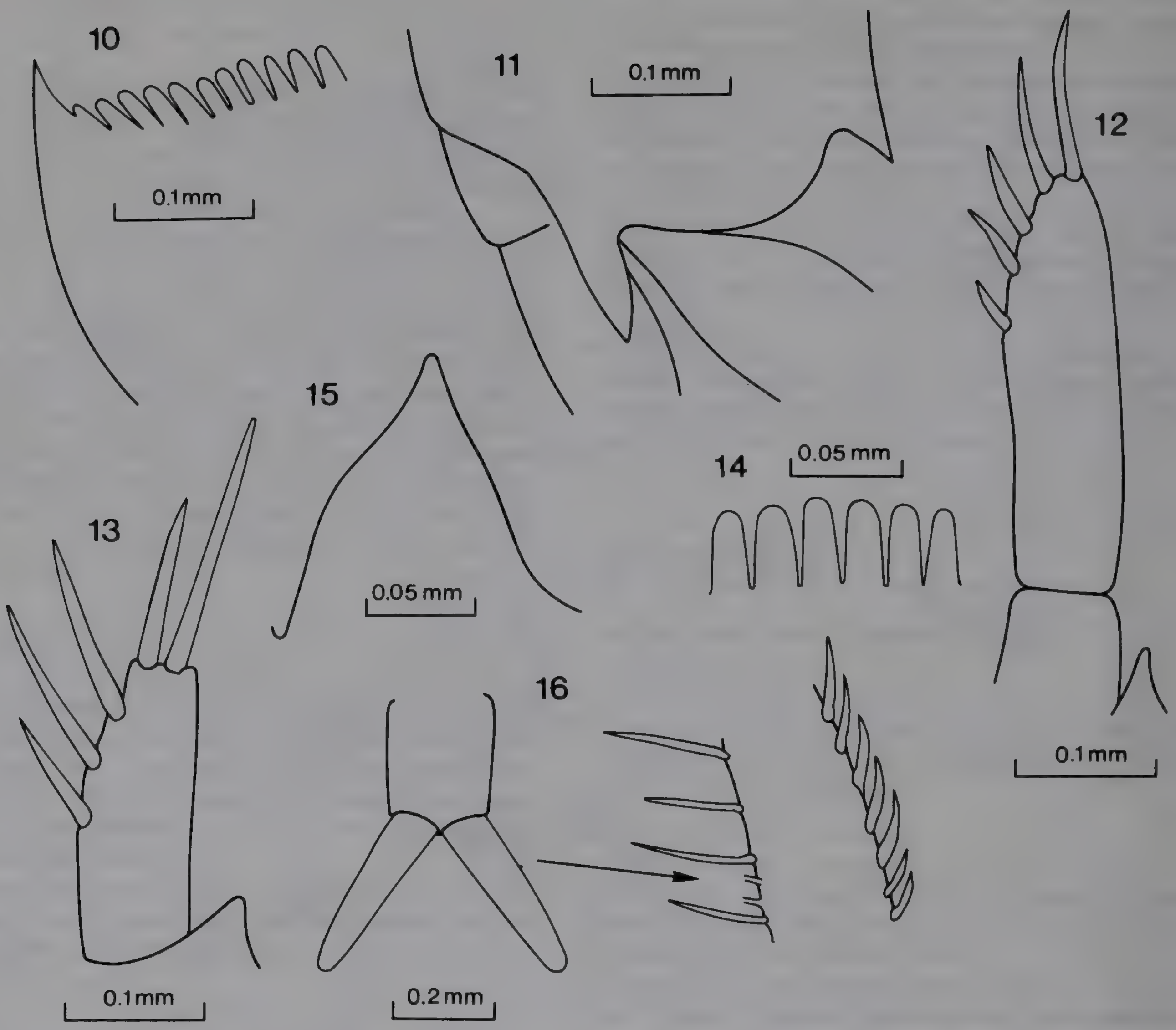
Figs 1–9 *Nebalia longicornis* G. M. Thomson, female lectotype. 1. Rostrum. 2. Compound eye. 3. Antennule. 4. Antenna. 5. Mandibular palp. 6. Maxillary palp. 7. 1st thoracopod. 8. 3rd thoracopod. 9. 1st pleopod.

distally. Of marginal spine-row only position of proximal spine indicated in fig. 5. Proximal 8 spines in marginal row shorter than the distal ones, the 9th spine intermediary.

2nd maxilla: (fig. 6) with distal article of palp of endopod only slightly shorter than proximal article. Exopod reaching past end of 1st article of endopod.

Thoracopods: Endopod of both 1st thoracopods broken distally (fig. 7). Exopod narrow, only as broad as basal part of endopod, epipod reaching to middle of exopod, 3rd thoracopod (fig. 8) with broad exopod, exopod reaching past middle of endopod.

Pleopods: Endopod of 1st pleopod only slightly shorter than peduncle. Terminal posterior spine on peduncle reaching past middle of row of marginal spines on exopod which is composed of about 22 spines. Distal to the spine-row there are 2 subterminal and 3 terminal spines (fig. 9); 4th pleopod

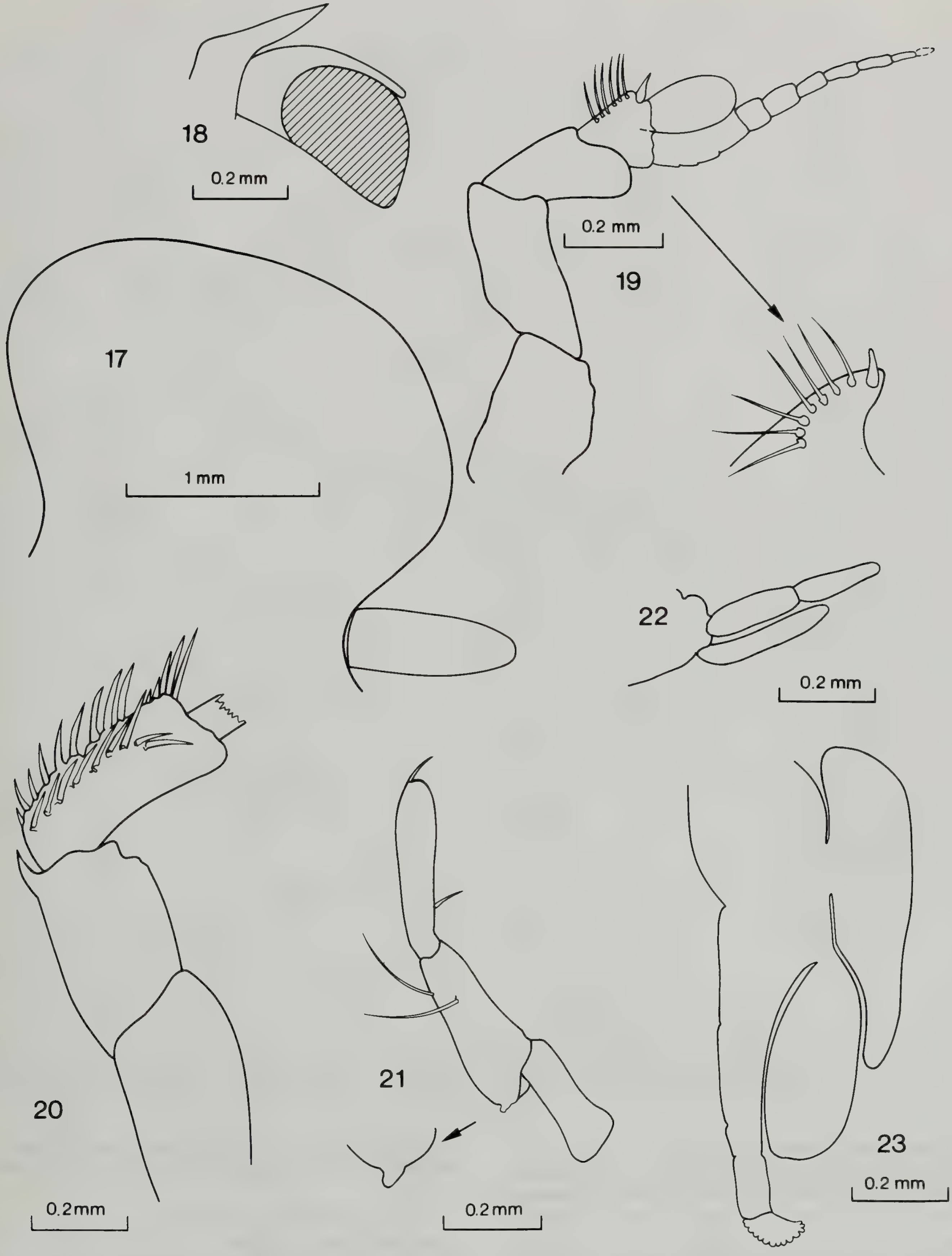


Figs 10—16 *Nebalia longicornis* G. M. Thomson, female lectotype. 10. 4th pleon segment epimeron. 11. 4th pleopod, distal part of peduncle and bases of endopod and exopod. 12. 5th pleopod. 13. 6th pleopod. 14. Crenelation on posterior dorsal margin of 7th pleon segment. 15. Anal scale. 16. Furcal rami with detail of armature.

(fig. 11) with posterolateral corner of peduncle produced and acutely pointed. Process in front of exopod attachment blade-shaped; 5th pleopod (fig. 12) with process between bases of rami short, narrowly triangular and with point sub-acute; 2nd article more than 3 times as long as wide, with 3 spines on distal third of lateral margin and 2 terminal spines (fig. 12); 6th pleopod (fig. 13) with process between rami forming a like-sided triangle, point sub-acute. Rami less than 3 times as long a wide, with 3 spines on distal half of lateral margin and 2 terminal spines.

COMPARISON between lectotype and postovigerous female, carapace length 2.4 mm, from sample in Museum of Victoria, locality unknown, brought from New Zealand by Mr. G. M. Thomson and labelled 'cootypes', specimen referred to below as 'Thomson specimen'.

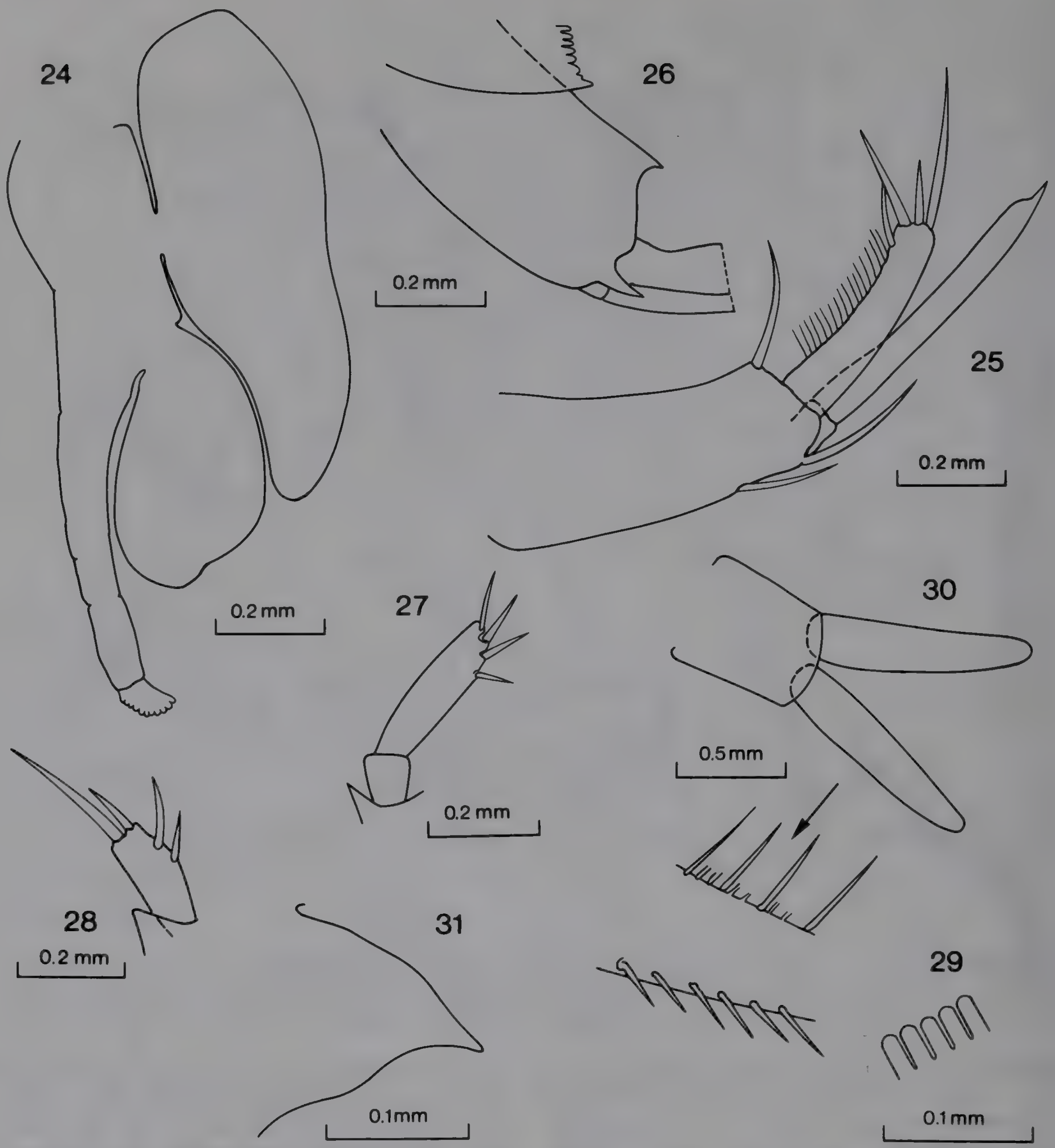
Rostrum: (figs. 1 and 17), general shape identical, greatest length/width ratio in both cases 2.6.
4th pleon epimeron: (figs. 10 and 26), identical.
Crenulation: on pleon segments 6 and 7 (figs. 14 and 29), identical.
Anal scales: (figs. 15 and 30), nearly identical.
Furca: (figs. 16 and 31), proportions similar, in lectotype setae between spines only on proximal part of medial margin, in Thomson specimen along whole margin.
Compound eyes: (figs. 2 and 18). General shape, eye papilla, and extension of ommatidial part practically identical.
Antennule: (figs. 3 and 19), closely similar.
Antenna: (figs. 4 and 20), similar but in both specimens minor variations in number of lateral spines on 3rd article of peduncle.
Mandibular palp: (figs. 5 and 21), proportions and armature identical.
2nd maxilla: (figs. 6 and 22), proportions and armature identical.
Thoracopods 1 and 3: (figs. 7, 8 and 23, 24), proportions practically identical.
Pleopods 1 and 4: (figs. 9, 10 and 27, 28), proportions and armature similar, process in front of exopod of pleopod 4 appears slightly more curved in Thomson specimen, which might be due to small differences in perspective.
Pleopods 5 and 6: (figs. 12, 13 and 27, 28), proportions similar, processes between rami identical in shape, but with point more acute in Thomson specimen. Lateral and distal marginal spines totalling 5 in lectotype and 4 in Thomson specimen.



Figs 17 –23 *Nebalia longicornis* , 'Thomson specimen'. 17. carapace valve and rostrum. 18. Compound eye. 19 Antennule. 20. Antenna. 21. Mandibular palp. 22. Maxillary palp. 23. 1st thoracopod.

As shown by this comparison the shape and proportion of parts are practically identical in both specimens. Minor differences in armature were observed, but such individual and growth related variations occur regularly in Nebalia (Dahl 1985).

The close similarity with respect to all morphological characters confirms that the lectotype and the Thomson specimen belong to the same species. The lectotype comes from Otago Harbour, where Thomson collected his original single specimen. The fact that Thomson made most of his collecting there makes it highly probable, although not possible to prove, that his 'cootypes' came from the same area. It is reasonable to conclude that the identity of *Nebalia longicornis* Thomson is now definitely established. The lectotype and paralectotypes of *N. longicornis* are in the New Zealand National Museum, Wellington.



Figs 24—31 *Nebalia longicornis* , 'Thomson specimen'. 24. 3rd thoracopod. 25. 1st pleopod. 26. 4th pleon segment epimeron and proximal part of 4th pleopod. 27. 5th pleopod. 28. 6th pleopod. 29. Crenelation on posterior margin of 7th pleon segment. 30. Telson and furca. 31. Anal scale.

ADDITIONAL MATERIAL EXAMINED

1. New Zealand, Otago Harbour, Portobello Marine Laboratory, locality B 7 (1) 6 fathoms, June 17, 1965, 1 specimen.
2. Same area, Loc. B 10_2, 6 fathoms, June 6, 1965, 1 specimen.

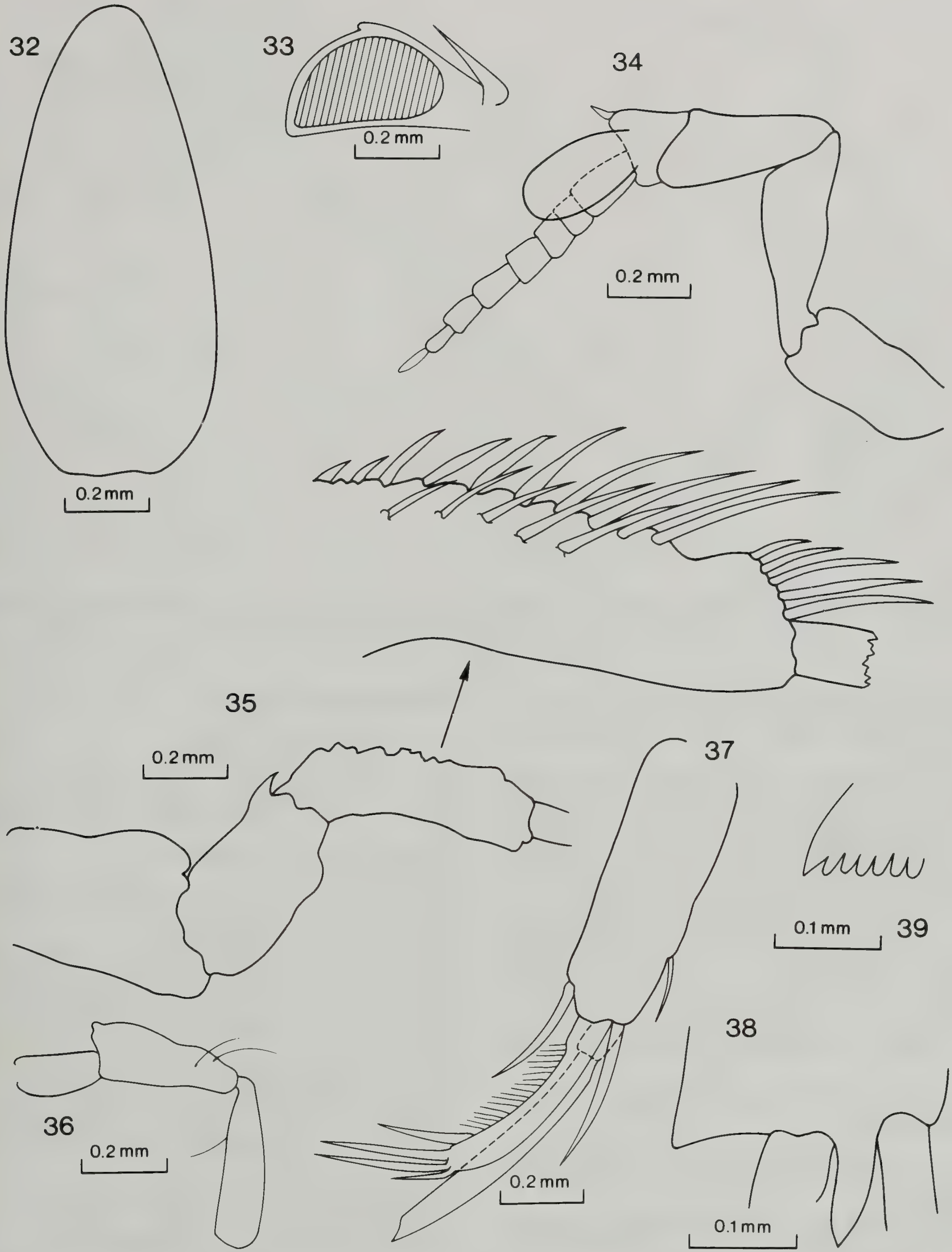
Nebalia patagonica n. sp.

Description of female holotype.

NOTE. The material of *N. patagonica* is not in a perfect condition. The 2nd maxilla and the thoracopods could not be separated in any of the specimens and are therefore not included in the description. Other diagnostic features are, however, available and permit a description leaving no doubts concerning the identity of the species.

TYPE LOCALITY: Tierra del Fuego, Canal Magdalena, Hope Harbour, 6–10 m, rocks with algae, April 30, 1894.

Status of female: Prae-ovigerous.
Carapace length: 2.5 mm.
Rostrum: (fig. 32) expanding slightly near base and then tapering evenly to a rather narrow, rounded point.
Pleon, telson, furca: Posterolateral corner of 4th pleon epimeron pointed but only slightly produced, denticles along posterior margin rounded (fig. 39). Denticles on posterior margin of pleon segments 6 and 7 tapering very slightly distally but with rounded tips (fig. 42). Anal scales (fig. 43) with medial margin broadly convex, point very short, over centre of scale, 'shoulder' broad and rather distinct. Furcal rami (fig. 44) hardly tapering distally and subequal in length to combined length of pleon segment 7 and telson.



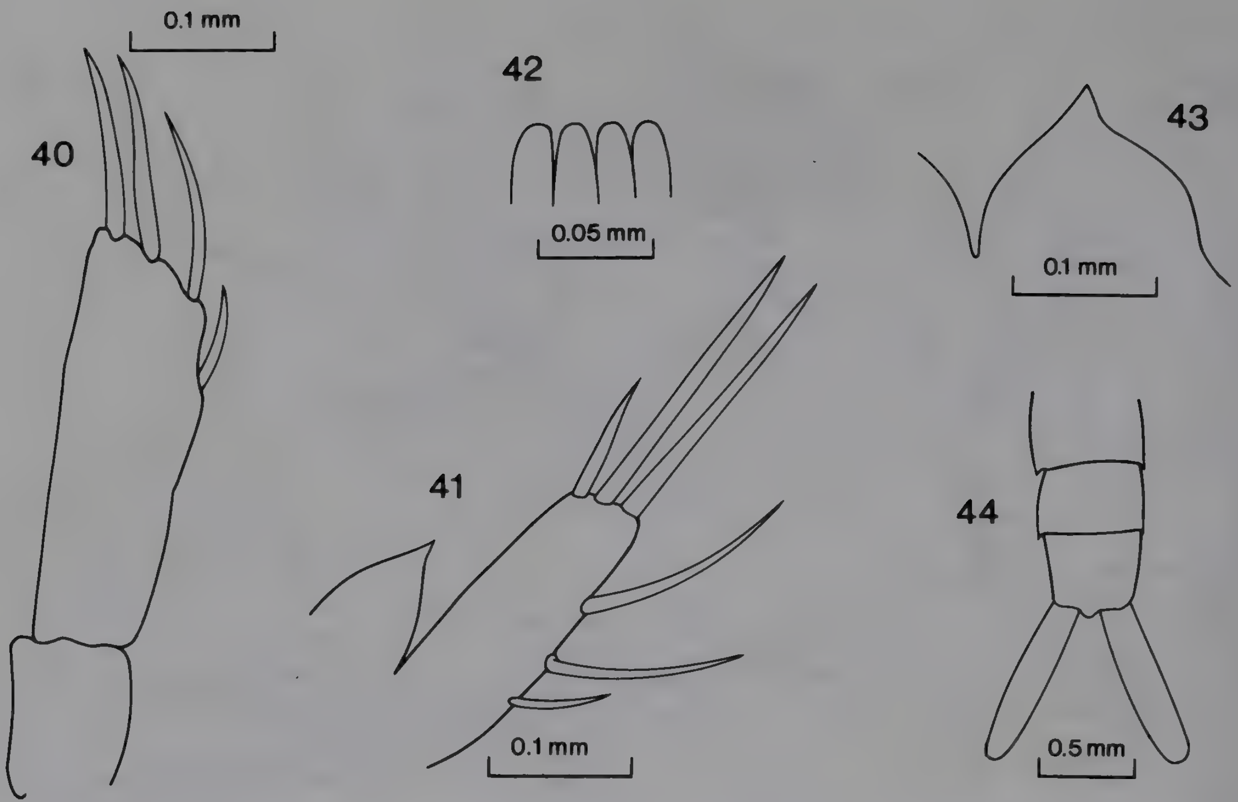
Figs 32—39 *Nebalia patagonica* n. sp., female holotype. 32. Rostrum. 33. Compound eye. 34. Antennule. 35. Antenna. 36. Mandibular palp. 37. 1st pleopod. 38. 4th pleopod. 39. 4th pleon segment epimeron.

Compound eye: (fig. 33) with small but distinct eye papilla. Ommatidial area covering more than 2/3 of the length of the eye-stalk. Supraorbital plate projecting past proximal ommatidia.

Antennule: (fig. 34) with 2nd article of peduncle slender and distinctly longer than 3rd article; 4th article with only 1 spine on distal dorsal corner. Antennular scale about twice as long as wide. Flagellum much shorter than peduncle, with 7 articles.

Antenna: (fig. 35) with 3rd article of peduncle distinctly longer than 2nd article. Lateral spine-row on 3rd article with fewer spines than marginal row, only 5 present in type.

Mandibular palp: (fig. 36) with 2nd and 3rd articles subequal in length, the 2nd article with small tubercle on proximal corner and one subterminal and one lateral seta, both of medium length; 3rd article distinctly expanded distally,



Figs 40—44 *Nebalia patagonica* n. sp. female holotype. 40. 5th pleopod. 41. 6th pleopod. 42. Crenelation on posterior dorsal margin of 7th pleon segment. 43. Anal scale. 44. Pleon, telson, furca.

lateral spine-row covering the distal 2/3 of the margin (cf. the position of the proximal spine indicated in fig. 36).

Pleopods: 1st pleopod (fig. 37) with lengths of peduncle and endopod subequal. Curved subterminal spine on posterior margin of peduncle reaching to centre of row of 17 short spines on margin of expod. Distally the exopod carries one subterminal and 3 terminal spines; 4th pleopod (fig. 38) with posterolateral corner of peduncle rectangular and not produced. Process in front of exopod base blade-shaped and nearly straight; 5th pleopod (fig. 40) with 2nd article about 3 times as long as wide and with only 1 lateral, 1 subterminal and 2 terminal spines; 6th pleopod (fig. 41) with ventral process between rami slightly pear-shaped and acutely pointed, 3 lateral spines set well apart and 3 terminal spines.

Holotype and paratypes in the State Museum of Natural History, Stockholm.

FURTHER MATERIAL EXAMINED: All samples come from the Magellan region.

1. Straits of Magellan, Punta Arenas, intertidal, sand under stones. 'Not rare'. 5 specimens. Dec. 2, 1896. Swed. Exp. to Tierra del Fuego.
2. Puerto Churruca, 20 fathoms, dead shells. 1 specimen. March 26, 1896. Swed. Exp. to Tierra del Fuego.
3. Fortescue Bay, 10–12 fathoms, algae. March 25, 1896. 1 specimen. Swed. Exp. to Tierra del Fuego.
4. Beagle Channel, Ushuaia, clay, 10 fathoms. May 5, 1896, 1 specimen. Swed. Exp. to Tierra del Fuego, and 6 m., clay, 1 specimen, Oct. 10, 1902 Swed. Antarct. Exp.

All these samples are in the State Mus. Nat. Hist., Stockholm.

TYPE: no. 3960

Nebalia antarctica n. sp.

Description of female holotype.

TYPE LOCALITY: Antarctic, Ross Sea, 'Discovery' Expedition, W. 2., no 4 hole, 4 fathoms, Jan, 10, 1903. 84 paratypes.

Status of female: Prae-ovigerous.

Carapace length: 5 mm.

Rostrum: (fig. 45). Sides nearly parallel, distally tapering slightly to broadly rounded apex.

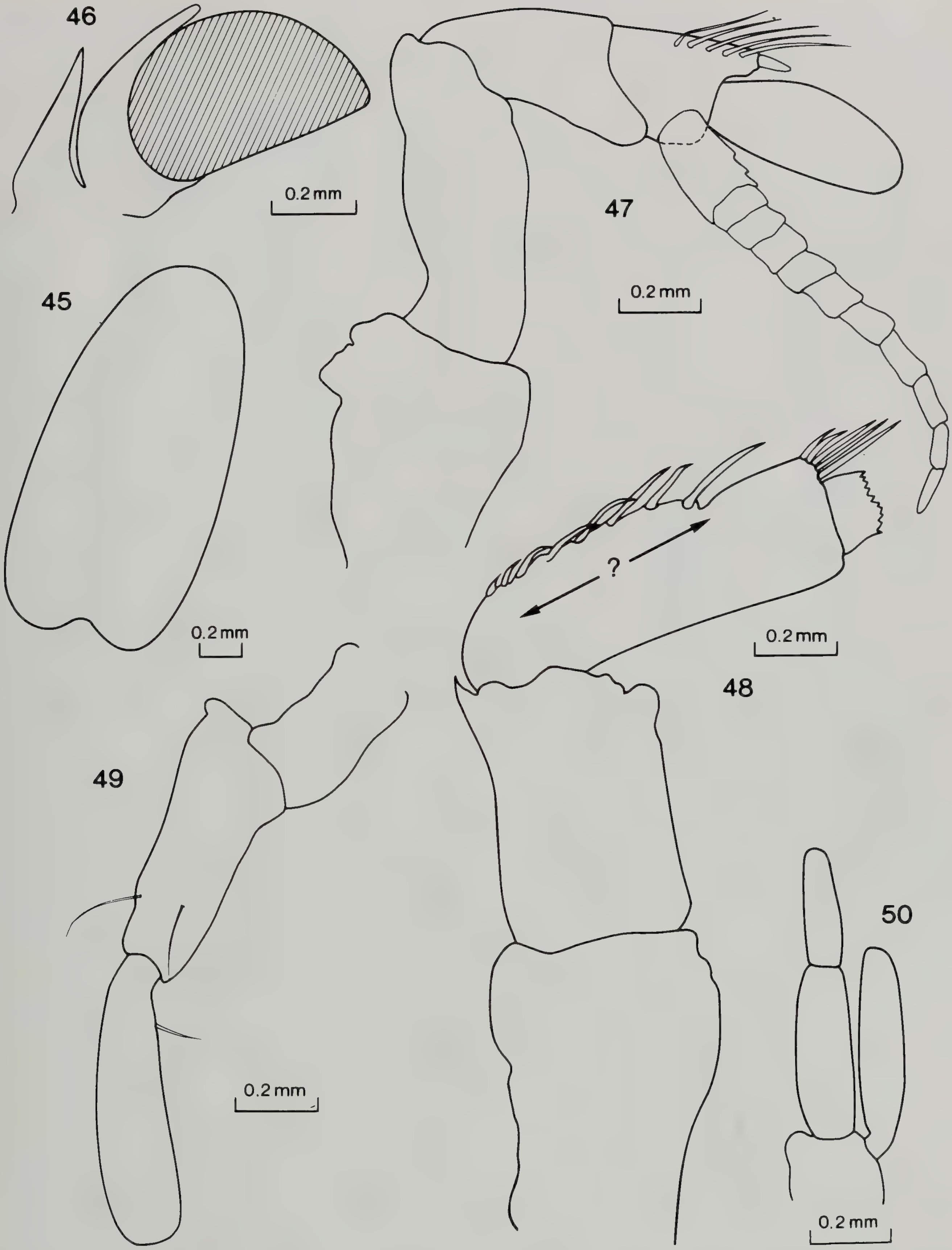
Pleon, telson, furca: Epimeron of 4th pleon segment with posterolateral corner produced and acutely pointed (fig. 56), denticles on posterior margin acutely pointed. Posteriodorsal margins of pleon segments with denticles tapering to acute points (fig. 61). Anal scales (fig. 62) with medial margin slightly concave and with long, acute points over medial part of scale. Lateral margins sloping steeply without distinct 'shoulders'. Furcal rami (fig. 63) tapering very slightly to rounded apices, slightly longer than combined length of 7th segment and telson.

Compound eye: (fig. 46) with ommatidial part covering 2/3 of eye-stalk. Eye papilla strongly developed, distal part produced, projecting freely over dorsum of eye. Supraorbital plate short, just reaching to level of proximal ommatidia.

Antennule: (Fig. 47) with 2nd article longer than 3rd article, 4th article with only 1 spine on distal corner. Antennular scale slightly more than twice as long as wide and with posterior margin nearly straight. Flagellum distinctly shorter than peduncle, with 11 articles.

Antenna: (fig. 48). 3rd article of peduncle rather short, only slightly longer than 2nd article. The details of the lateral spine-row could not be studied.

Mandibular palp: (fig. 49) with 2nd and 3rd articles nearly equal in length, the 3rd article slightly longer; 2nd article with



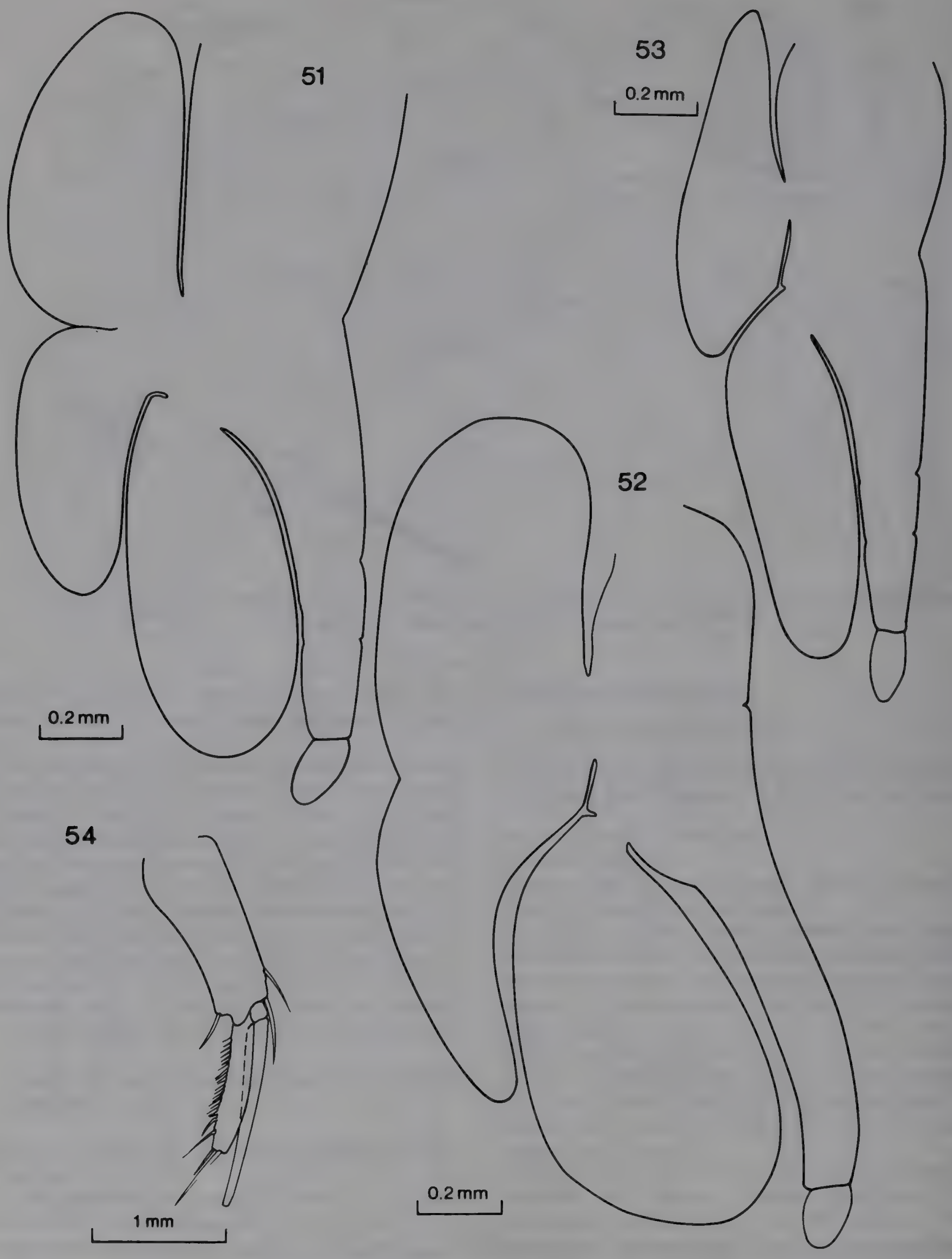
Figs 45—50 *Nebalia antarctica* n. sp., female holotype. 45 rostrum. 46. Compound eye. 47. Antennule. 48. Antenna. 49. Mandibular palp. 50. Maxillary palp.

small tubercle on proximal corner. One short subterminal seta on margin and one short lateral seta, 3rd article expanding distally, marginal spine-row along approximately 4/5 of margin (cf. position of proximal spine in fig. 49).

2nd maxilla: (fig. 50), distal article of endopod palp more than 2/3 the length of 1st article, exopod reaching beyond apex of 1st article.

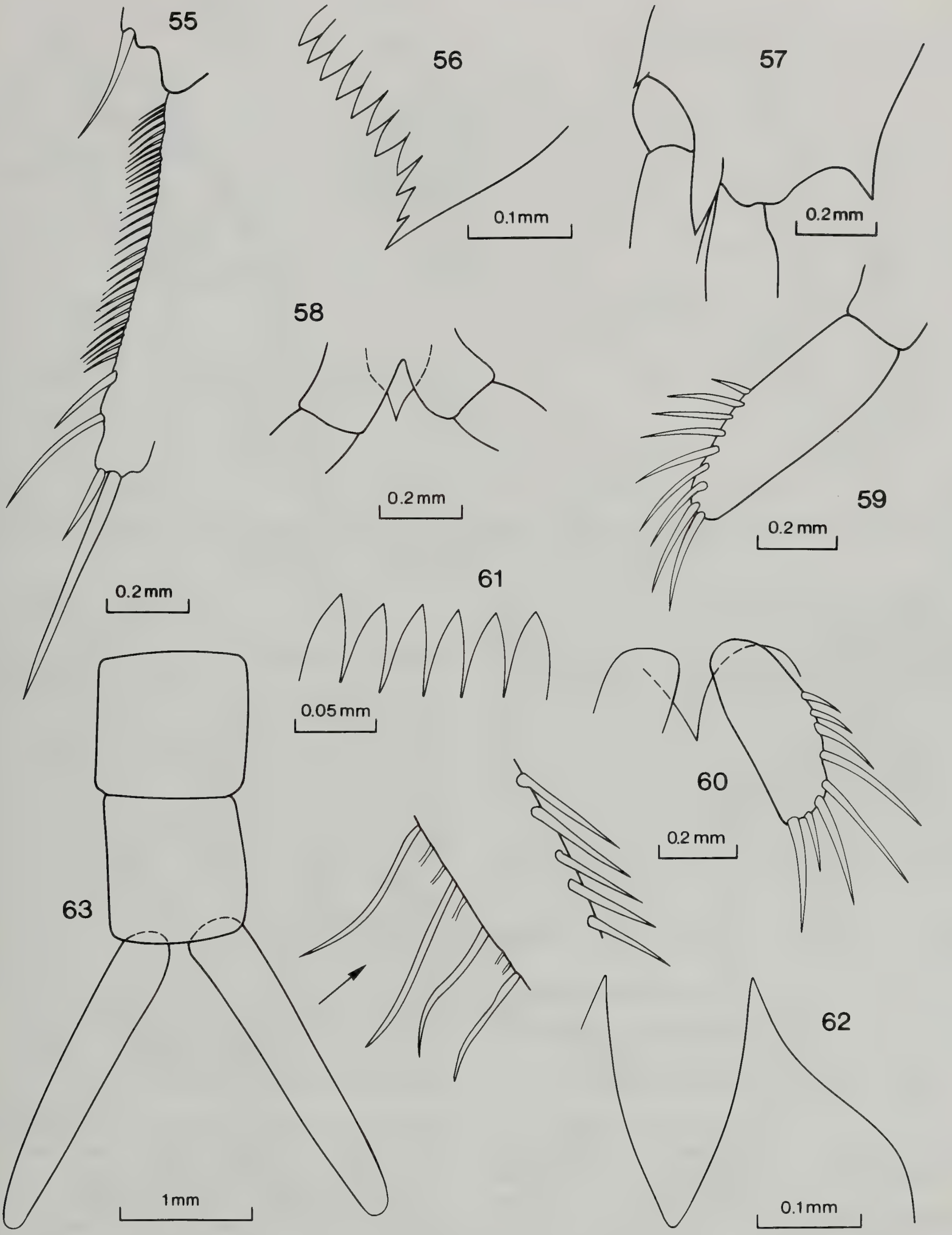
Thoracopods: 1st thoracopod (fig. 51) with exopod reaching level of base of endopod terminal article, epipod reaching to middle of exopod. Third thoracopod (fig. 52) with broad exopod reaching nearly to end of endopod. Distal lobe of epipod reaching beyond middle of exopod. Eighth thoracopod (fig. 53) with narrow, parallel-sided exopod reaching beyond base of terminal endopod article, epipod with distal lobe very short.

Pleopods: First pleopod (fig. 54) long and slender, endopod



Figs 51—54 *Nebalia antarctica* n. sp., female holotype. 51. 1st thoracopod. 52. 3rd thoracopod. 53. 8th thoracopod. 54. 1st. pleopod.

slightly longer than peduncle, exopod strikingly long, more than 2/3 the length of endopod. Subterminal spine on posterior margin of peduncle short, reaching only to level of the proximal part of marginal spine-row of exopod. The spine-row is long, composed of about 30 short spines (fig. 55). Distal to the spine-row there are 2 lateral and 2 terminal spines. Fourth pleopod with posterolateral corner of peduncle produced and acutely pointed, process in front of exopod base straight and blade-shaped (fig. 57). Fifth pleopod (fig. 58) with ventral process between rami pear-shaped and produced to form acute point. Rami short and comparatively broad (fig. 59) with dense row of short spines on distal half of lateral margin, composed of 7 lateral and 2 distal spines. Sixth pleopod (fig. 60) with process between



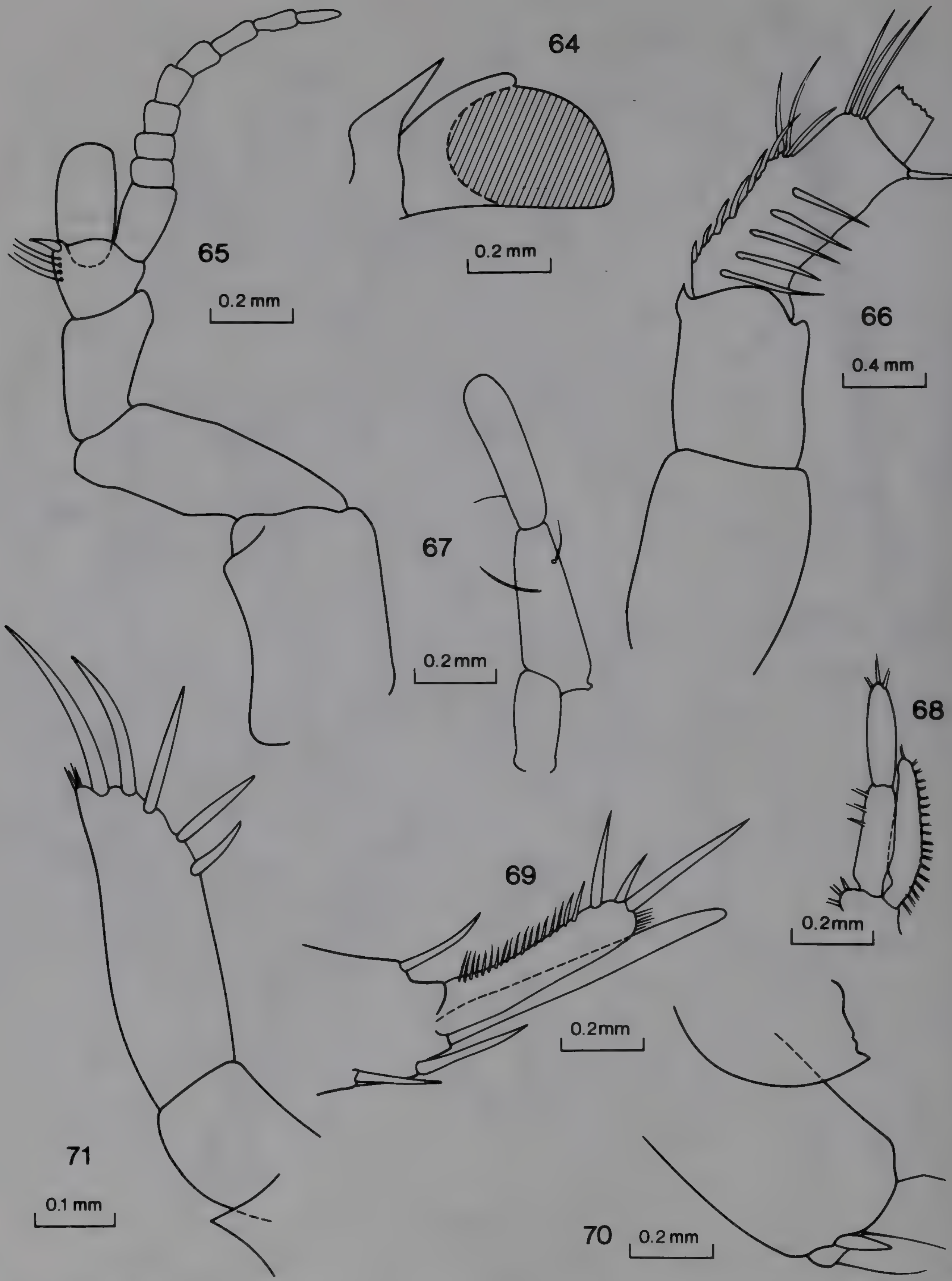
Figs 55—63 *Nebalia antarctica* n. sp., female holotype. 55. Exopod of 1st pleopod. 56. 4th pleon segment epimeron. 57. Proximal part of 4th pleopod. 58. Basis of 5th pleopod. 59. Ramus of 5th pleopod. 60. 6th pleopod. 61. Crenelation on posterior dorsal margin of 7th pleon segment. 62. Anal scale. 63. Telson and furca with detail of armature.

rami acutely pointed, a dense row of lateral and terminal spines covers more than half the lateral margin of ramus, composed of 9 spines.

Type and paratypes in British Museum (Nat. Hist.), London, type no. 1988: 95

FURTHER MATERIAL EXAMINED

1. 'Discovery' Exp. Winter Quarters, Hut Point, D. net, Oct. 1, 1902, 1 specimen.
2. Same locality, No. 6 Hole, 130 fathoms, Feb. 2, 1903. 1 specimen.
3. Same locality without further data. 1 specimen and 2 specimens.



Figs 64—71 *Nebalia falklandensis* n. sp., female holotype. 64. Compound eye. 65. Antennule. 66. Antenna. 67. Mandibular palp. 68. Maxillary palp. 69. 1st pleopod. 70. 4th pleon segment epimeron and proximal part of 4th pleopod. 71. 5th pleopod.

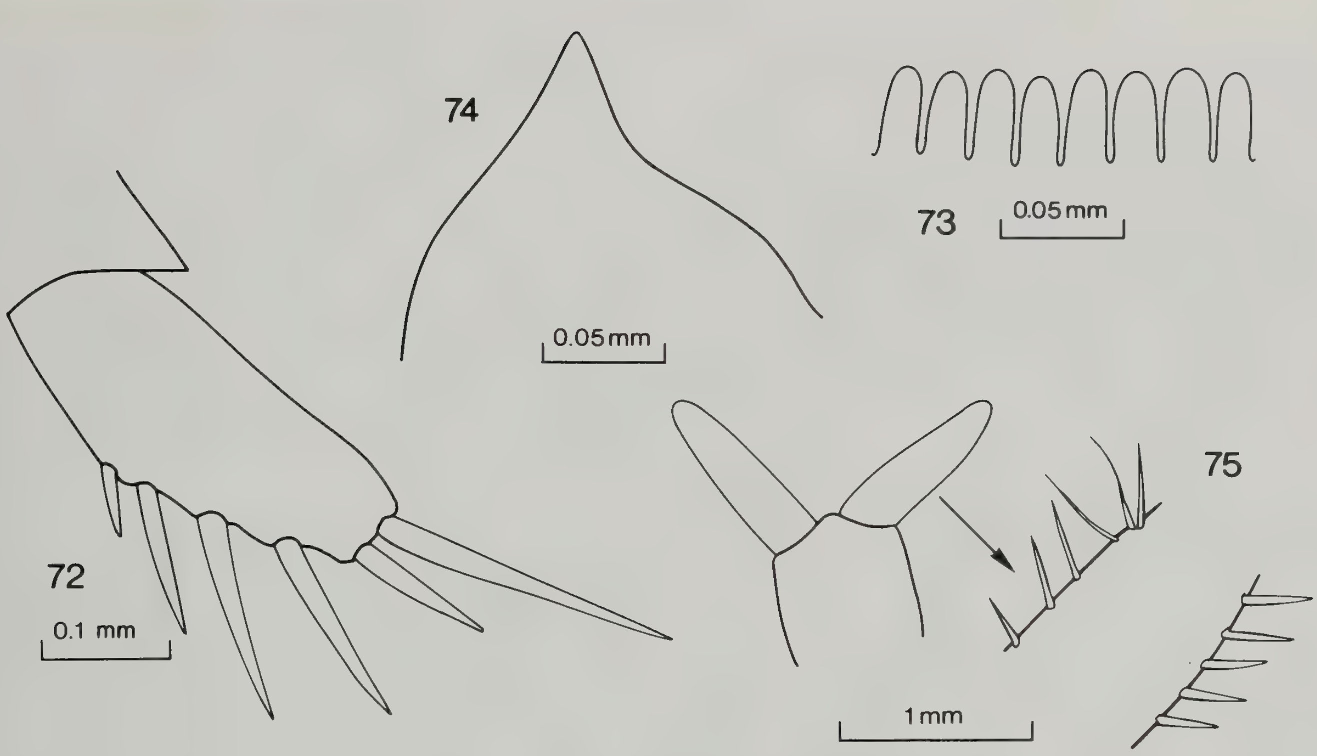
4. 'Terra Nova' st. 331. 1 specimen.
5. King George V Land, Commonwealth Bay, Boat Harbour, 5 fathoms, June 6, 1912 1 specimen.

FURTHER DISTRIBUTION: Antarctic, Wilhelm II Land and Adélie Land.

Nebalia falklandensis n. sp.

Description of female holotype.

TYPE LOCALITY: Falkland Islands, 'Discovery', St. 51, off Eddystone Rock, May 14, 1926, only holotype.



Figs 72—75 *Nebalia falklandensis* n. sp., female holotype. 72. 6th pleopod. 73. Crenelation on posterior dorsal margin of 7th pleon segment. 74. Anal scale. 75. Telson and furca with detail of armature.

Status of female: Prae-ovigerous.
Carapace length: 2.6 mm
Rostrum: removed and measured by Cannon (1931), length/width ratio reported to be 2.07:1.
Pleon, telson, furca: Epimeron of 4th pleon segment with posterolateral corner produced to form a short and not very acute point, posterior margin somewhat irregular, possibly slightly damaged (fig. 70). Crenulation on posterio-dorsal margin of pleon segments 6 and 7 with denticles broadly rounded (fig. 73). Anal scales (fig. 74) short with point somewhat closer to medial margin, 'shoulder' broad and rather distinct. Furca (Fig. 75) with rami short, not much longer than telson and gradually tapering.
Compound eye: (fig. 64) with short eye-stalk, ommatidial part covering nearly 4/5 of its length. Eye papilla distinct but not produced over dorsum of eye. Supraorbital plate covering proximal ommatidia.
Antennule: (fig. 65) with 2nd article of peduncle nearly twice as long as 3rd article, 4th article with only one spine on distal corner. Antennular scale about twice as long as wide, ventral margin nearly straight. Flagellum about half as long as peduncle, with 11 articles.
Antenna: (fig. 66) with 3rd article about 1.5 times as long as 2nd article, lateral spine-row with 5 spines.
Mandibular palp: (fig. 67) with 2nd and 3rd articles subequal, 2nd article with small tubercle on proximal corner and with one short subterminal and one lateral seta; 3rd article hardly expanding distally. Marginal spine-row covering about 4/5 of margin (note position of proximal spine in fig. 67).
Maxilla: (fig. 68) with 1st article of endopod only very slightly longer than 2nd article. Exopod reaching well beyond apex of 1st article.
Thoracopods In order to evade excessive damage to the unique specimen the thoracopods were not dissected.
Pleopods: First pleopod (fig. 69) with peduncle slightly longer than endopod. Subterminal spine on the posterior margin of peduncle short, reaching only to level of proximal part of spine-row on exopod. This spine-row is rather short and composed of 19 spines only, the distal ones clearly stronger than the others. Distal to the spine-row there are 2 lateral, 1 subterminal, and 1 terminal spine. Fourth pleopod (fig. 70) with posterolateral corner of peduncle truncate. The process in front of the exopod is short and acutely pointed. Fifth pleopod (fig. 71) with the process between rami triangular and acutely pointed. Ramus with distal article 3 times as long as wide, with a row of 3 lateral spines on distal part of margin and 2 somewhat longer terminal spines. Sixth pleopod with process between rami acutely pointed (fig. 72). Ramus not much more than twice as long as wide; 4 spines on distal half of lateral margin and 2 terminal spines.

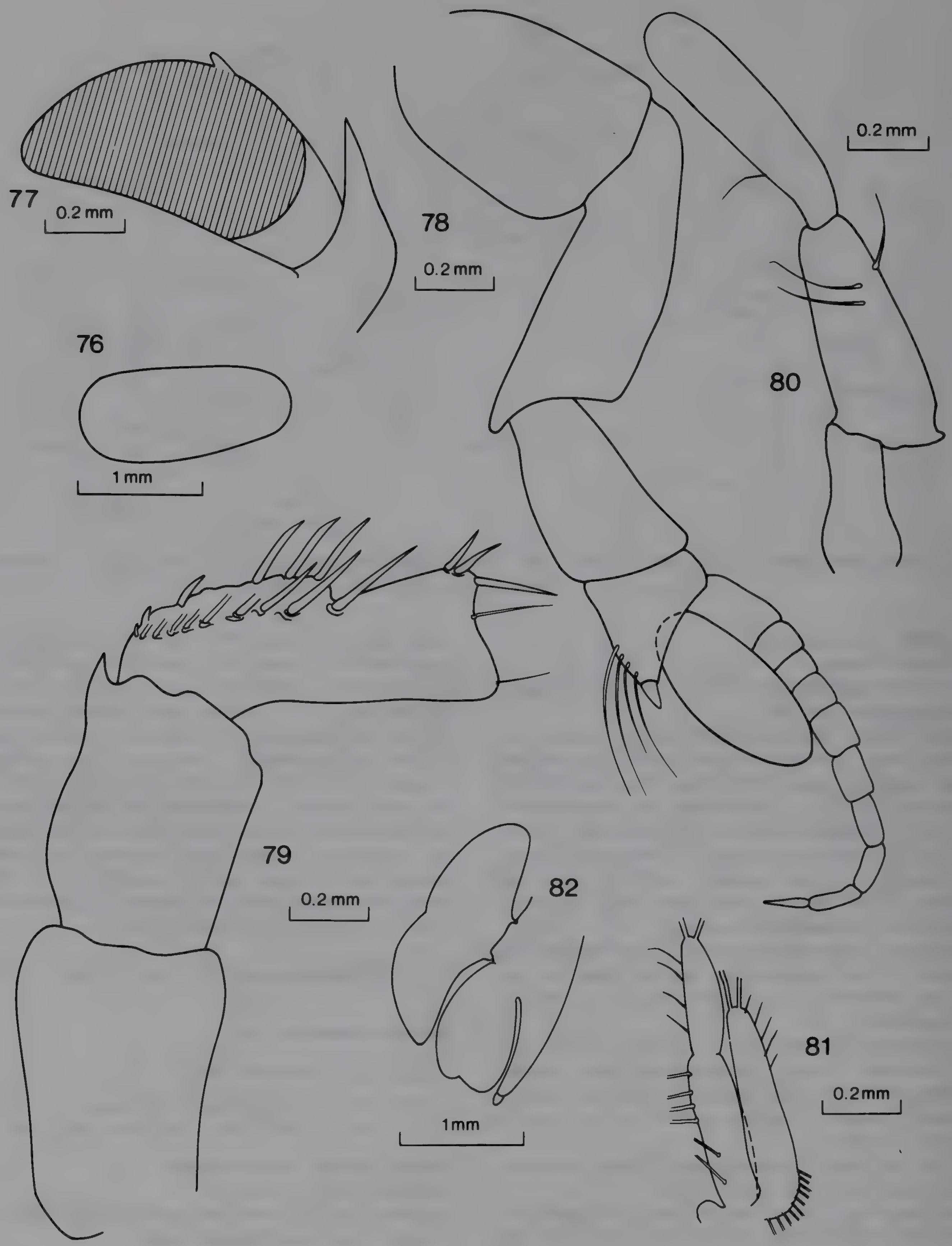
Type in British Museum (Nat. Hist.). Type no. 1988:97

Nebalia cannoni n. sp.

Description of female holotype.

TYPE LOCALITY: South Georgia, 'Discovery' st. 144, 54°04'—53°38' S, 36°27'—36°26' W, 155–178 m Jan. 5, 1927.

Status of female: Prae-ovigerous.
Carapace length: 5.5 mm.
Rostrum: (fig. 76) with sides nearly parallel, distally tapering abruptly to a broadly rounded apex.
Pleon, telson, furca: Epimeron on 4th pleon segment (fig. 84) with posterolateral corner produced and pointed. Posterior margin denticulate, distal denticles very narrow, the more proximal ones rounded to sub-acute. Denticles on posterior dorsal margin of 6th and 7th pleon segments (fig. 87) not very closely packed, sub-acute. Anal scales (fig. 88) with long, blunt point over medial part of scale, lateral margin sloping nearly evenly without distinct 'shoulder'. Furcal rami (fig. 89) tapering very slightly, subequal to combined length of telson and 7th pleon segment.
Compound eye: (fig. 77) large, with ommatidial part covering



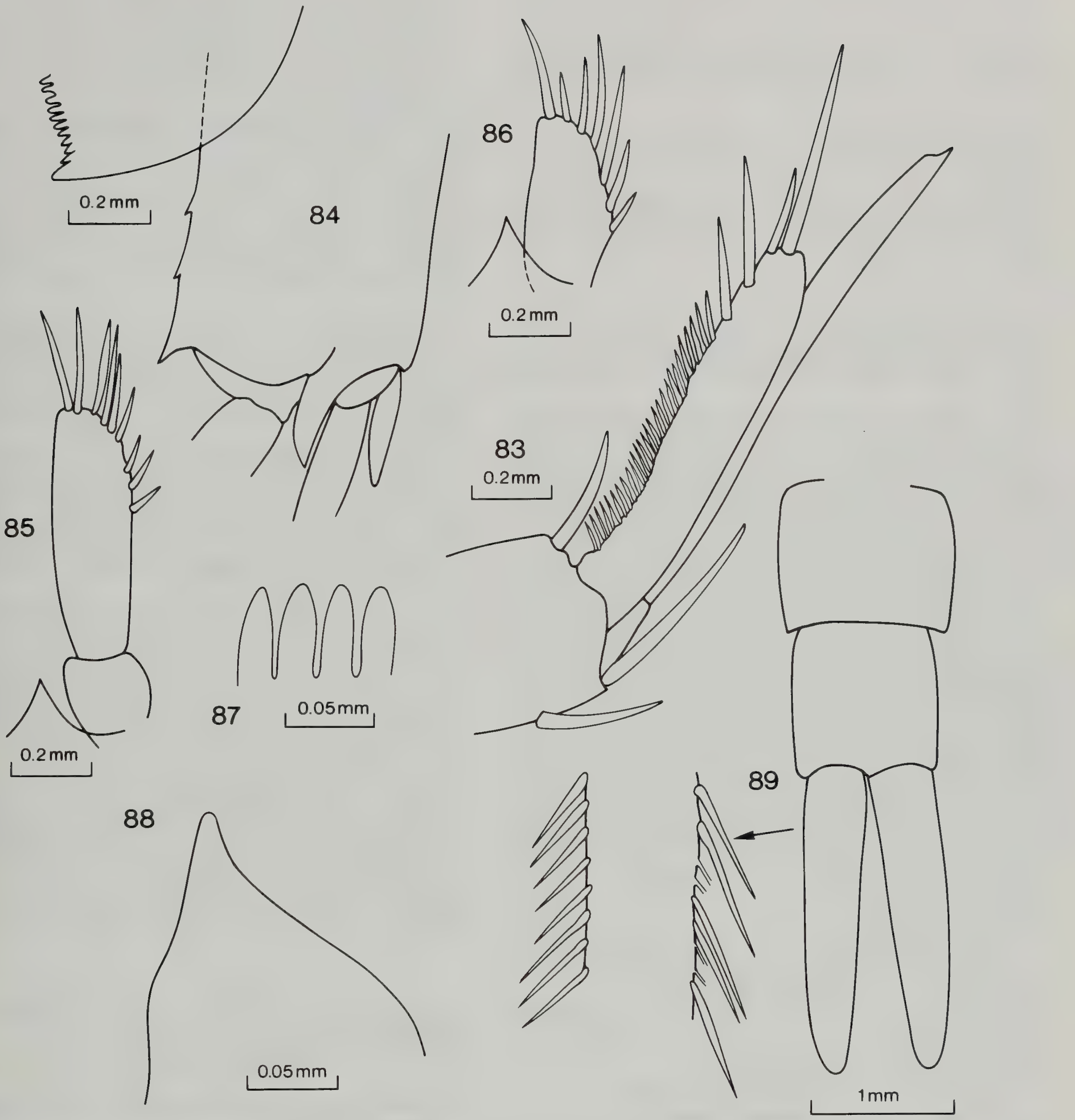
Figs 76–82 *Nebalia cannoni* n. sp., female holotype. 76. Rostrum. 77. Compound eye. 78. Antennule. 79. Antenna. 80. Mandibular palp. 81. Maxillary palp. 82. 3rd thoracopod.

nearly the whole eye-stalk. Eye papilla well developed and projecting freely over dorsum of eye. Supraorbital plate short.

Antennule: (fig. 78) with 2nd article of peduncle about 1.5 times as long as 3rd article, 4th article with only one spine on distal corner. Antennular scale elliptical and about 2.3 times as long as wide. Flagellum much shorter than peduncle, with 10 articles.

Antenna: (fig. 79) with 2nd article of peduncle about 4/5 the length of 3rd article. Lateral spine-row on 3rd article commencing proximally with some setae, gradually replaced by spines distally. Total number of spines and setae 10. Flagellum longer than peduncle.

Mandibular palp: (fig. 80) with 3rd article slightly longer than 2nd article, 2nd article with small tubercle on proximal corner and with one short subterminal seta and 2 lateral setae, 3rd



Figs 83—89 *Nebalia cannoni* n. sp., female holotype. 83. 1st pleopod. 84. 4th pleon segment, epimeron and proximal part of 4th pleopod. 85. 5th pleopod. 86. 6th pleopod. 87. Crenelation on posterior dorsal margin of 7th pleon segment. 88. Anal scale. 89. Telson and furca with detail of armature.

article slightly expanding distally. Marginal spine-row covering 2/3 of lateral edge, position of proximal spine indicated in fig. 30.

Maxilla: (fig. 81). Second article of endopod about 2/3 length of 1st article, exopod reaching nearly to middle of 2nd endopod article.

Thoracopods: (fig. 82). Thoracopods 2–7 with exopod and epipod large. Endopod proportionally short, reaching just past exopod.

Pleopods: First pleopod (fig. 83) with peduncle and endopod subequal in length. Subterminal spine on peduncle posterior margin not reaching to centre of spine-row on exopod. Exopod proportionally long, spine-row with about 30 spines, distally with 2 lateral and 2 terminal spines. 4th pleopod (fig. 84) with posterolateral corner of peduncle produced to form an acute point, its posterior margin with a few denticles. Fifth pleopod with process between rami short and acutely pointed, 2nd article of rami about 3 times as long as wide, with a row of short spines along distal part of lateral margin, totalling 9 lateral and terminal spines (fig. 85). Sixth pleopod (fig. 86) with process between rami short and acutely pointed, rami short and nearly triangular, with a row of 7 spines along distal two thirds of lateral margin.

Holotype in British Museum (Nat. Hist.), London, paratypes in Institute of Oceanographic Sciences, Wormley, Godalming, England. Type no. 1988:96.

FURTHER MATERIAL EXAMINED

South Georgia, 'Discovery' St. 45, 2.7 miles S. Jason Light, 238–270 m. April 6, 1926. 1 specimen.

This species is dedicated to the late Professor H. G. Cannon in recognition of his important contributions to the knowledge of the Leptostraca.

DISCUSSION AND CONCLUSIONS

For a long time it has been recognized that the taxonomy of *Nebalia* in the Southern Oceans has been very unsatisfactory (cf. Calman 1917, 1927, Cannon 1931, Johnson 1970). The re-discovery of *N. longicornis* Thomson (see p. 73) has now made this critical revision possible. The inclusion of numerous morphological features not considered by any previous author, except to some extent Barnard (1914), has also contributed materially to the new results presented here.

The long-prevailing unsatisfactory state originated from Thiele's (1904) misidentification of a juvenile nebalid as *N. longicornis*, now known to be a *Sarsinebalia* species. On this conclusion (and also the acceptance of Claus' (1887) wide species concept of leptostracans), Thiele based his comprehensive discussions on the taxonomy of *Nebalia* species and thus created difficulties for later workers. In the revision here at least 10 distinct species are recognized as having previously figured under the name *'N. longicornis'*. Of these it has been possible to identify 4 with sufficient certainty to describe them as new species and also to present a revised list of the southern hemisphere *Nebalia* species as follows:

1. Established species:
   N. longicornis G.M. Thomson (1879), SE New Zealand
   N. capensis K.H. Barnard (1914), S. Africa
   N. ilheoensis Kensley (1976), SW Africa
   N. strausi Risso (1826), St. Helena, NE Atlantic, W Mediterranean
   N. patagonica n. sp., Magellan Region
   N. antarctica n. sp., Antarctic coastal waters
   N. falklandensis n. sp., Falkland Islands
   N. cannoni n. sp., S. Georgia
2. Species for which published observations indicate that they are new to science without permitting a description:
   N. sp., New Britain, Blanche Bay (Thiele 1904)
   N.. sp., Brazil, Ubatuta (Wakabara 1964)
   N. sp., Singapore, (Johnson 1970)
3. Records without further relevant information:
   N. chilensis (Claus 1887). *Nomen nudum*, most probably a new species
   N. sp. Loyalty Islands, Lifu. (Thiele 1904, *'Nebalia longicornis'*)

This more realistic species concept of the genus *Nebalia* has materially increased the number of southern hemisphere species but these must represent only a small fraction of *Nebalia* species present in the region. Previous studies on N. E. Atlantic nebalids (see Dahl, 1985) combined with unpublished observations on collections from N. W. Atlantic, N. E. Pacific and Australian regions, indicate that the numbers of leptostracan species for these respective areas are far fewer and more restricted than, for example, isopods, amphipods, cumaceans and tanaidaceans occurring in comparable habitats.

The Leptostraca and their extinct phyllocarid relatives date back to the Ordovician and have conserved many primitive features. They provide us with a most important source of information concerning early malacostracans. Hopefully the present elucidation of some taxonomic problems will facilitate future critical research on various aspects of leptostracan biology in the Southern Hemisphere.

ACKNOWLEDGEMENTS. The present study was supported by grants from the Swedish Natural Science Research Council and the Royal Physiographic Society, Lund, and by the granting of facilities at the Department of Zoology, University of Lund by Professor Rolf Elofsson.

My cordial thanks are due to Dr G. C. B. Poore, Museum of Victoria, for trusting me with the examination of the specimens of *Nebalia longicornis* brought to Australia by Mr G. Thomson, which gave the impetus to the present investigation, and to Professor J. B. Jillett, Portobello Marine Laboratory, New Zealand, for the specimens from Otago Harbour from which the lectotype of *N. longicornis* was selected.

I am greatly indebted to Miss Joan Ellis, Crustacea Section, British Museum (Nat. Hist.) for her untiring help and patience, to Dr Michael Thurston and Miss K. G. Chidgey, Inst of Oceanographic Sciences, Godalming for making available 'Discovery' collections, to Professor Torben Wolff, University of Copenhagen for access to the specimen of *Sarsinebalia* which provided the key to the discussions by Thiele (1904, 1905), and to Mr Roy Oleröd, State Museum of Natural History, Stockholm, for the material of *N. patagonica*. Miss Ylwa Andersson and Mrs Gunilla Bergh helped me with many practical problems, and my special thanks are due to Mrs Astrid Ulfstrand for invaluable help in making my drawings ready for publication.

Last but not least my cordial thanks are due to Dr Roger Lincoln for seeing this paper through the press and to Dr R. W. Ingle for highly appreciated criticism and many linguistic improvements.

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Manuscript accepted for publication 13th July 1989

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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

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ISBN 0 565 05048 6
ISSN 0007 – 1498

Zoology Series
Vol 56 No 2 pp 93 – 204

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 25 October 1990

Typeset by J & L Composition, Filey, North Yorkshire
Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

Bull. Br. Mus. nat. Hist (Zool.) **56**(2): 93–103 Issued 25 October 1990

Tinogullmia riemanni sp. nov. (Allogromiina; Foraminiferida), a new species associated with organic detritus in the deep-sea

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INTRODUCTION

Recent studies, carried out in the northeast Atlantic as part of the benthic biology programme at the Institute of Oceanographic Sciences Deacon Laboratory (IOSDL), have shown that benthic foraminifera, together with nematodes, are the dominant organisms in the meiofaunal (42–1000µm) size range (Gooday 1986*b*, 1988*a*, Gooday & Lambshead 1989). The foraminiferal populations are highly diverse and include many new taxa, among them members of the Allogromiina (Gooday 1986*b*). This suborder includes foraminifera with morphologically simple tests composed of proteinaceous material which is often flexible and transparent (Loeblich & Tappan 1988). Because they have delicate tests and are easily overlooked or destroyed during the processing and sorting of samples, allogromiins are the least well-known of the main foraminiferal suborders. In particular, few species have been reported from the deep-sea (Gooday 1986*a*).

The purpose of this paper is to describe a new allogromiin which is abundant in samples from the abyssal and bathyal northeast Atlantic. The new species is of special interest because of its association with organic detritus.

MATERIALS AND METHODS

The material described was collected with a multiple corer (Barnett *et al.*, 1984) at two localities. The bathyal site (51° 36′N, 13° 00′W, 1350m) is located in the Porcupine Seabight, an embayment of the continental shelf to the southwest of Ireland. It was sampled during RRS *Challenger* cruise 10/82 (Stn 51615, 22–23 July 1982). The abyssal site (4500m) was sampled during the third cruise of the German research vessel FS *Meteor* (Stns 172, 179, 200; 7–14 August 1986). It is located in the BIOTRANS box (47° 00′–47° 30′N, 19° 00′–20° 00′W), an area which has been subject to an intensive investigation by the Institut für Hydrobiologie und Fischereiwissenschaft, Universität Hamburg.

Nine sediment subsamples (identified as 1A, 1B etc; see Gooday & Lambshead 1989) from the cores collected at Stn 51615 were washed through a series of sieves and the resulting residues stained with rose Bengal and sorted wet under a binocular microscope. In the case of the BIOTRANS samples, aggregates of organic detritus, which provide a microhabitat for the new species, were lifted from the core surfaces using forceps. Later, in the laboratory, they were gently teased apart in a cavity block or cavity slide to release the inhabiting organisms. Allogromiin foraminifers extracted from these samples were mounted in anhydrous glycerine on a glass slide under a supported cover slip sealed with D.P.X. For further details of sampling and processing methods see Gooday (1986*a*, 1986*b*, 1988*a*, 1988*b*, Gooday & Lambshead 1989).

Drawings were made using a Wild M20 drawing tube. Photographs were taken on an Olympus BH2 photomicroscope and the results recorded on Ilford FP4 film.

SYSTEMATIC DESCRIPTIONS

Suborder **ALLOGROMIINA** Loeblich & Tappan, 1961
Family **ALLOGROMIIDAE** Rhumbler, 1904
Subfamily **SHEPHEARDELLINAE** Loeblich & Tappan, 1984

Genus **TINOGULLMIA** Nyholm, 1954
Tinogullmia riemanni sp. nov.

1988*a* Allogromiid sp. Gooday: p. 72, Fig. 1a, 1b.

DIAGNOSIS. Small species of *Tinogullmia* (<300µm long) with elongate, lenticular, usually asymmetrical test, tapering at both ends. Apertures located at extremities of short necks which extend out from ends of test. Wall delicate, transparent, proteinaceous. Protoplasm fairly homogenous and free from obvious detrital particles; usually with single large nucleus.

Name. In honour of Dr Franz Riemann who was the first to observe this species in phytodetritus aggregates on board the *Meteor*.

Material. 81 specimens from *Meteor* Stn 172 (47° 25.35′N, 19° 39.46′, 4438m depth); 102 specimens from *Meteor* Stn 179 (47° 24.95′N, 19° 48.00′W, 4538m depth); 102 specimens from *Meteor* Stn 200 (47° 24.16′N, 19° 45.65′W, 4520m); 171 specimens from *Challenger* Stn 51615 (51° 35.1′–51° 36.0′N, 12° 59.3′–13° 00.6′W, 1345–1361m). The *Challenger* material is in the author's collection at IOSDL.

Holotype. The holotype and 37 paratypes, from phytodetritus collected at *Meteor* Stn 179 (core 1), are deposited in the Natur-Museum Senckenberg, Frankfurt am Main, under reg. no. SMF 1086 (one slide). Twenty-one additional paratypes are deposited in the British Museum (Natural History), London under reg. nos ZF4783–4793 and ZF4794–4803 (two slides).

Description. (*Meteor* material; Figs 1a–xx, 2a–s; 3a–l; 8a, b, e). Test dimensions are summarised in Table 1 and test length is plotted against height in Fig. 4. The test is elongate, approximately circular in cross-section, with apertures located at the ends of short tubes which extend out from either end of the test. The tubes are 2.7–13.3μm long (usually 4.0–10.7μm, mean 5.8 ± 2.1μm, 172 observations) and 4.0–10.7μm wide (mean 6.0 ± 7.0μm, 77 observations). In principle, most specimens are lenticular in lateral outline and taper towards the apertural tubes. The outline is usually (>80% of specimens) asymmetrical with one side forming a convex arc and the other side ranging from gently convex to gently concave. The maximum height is generally situated near the midpoint of the test but sometimes lies slightly nearer one end. In most cases, the apertural tubes are located below a line drawn through the mid-point of the test and usually are directed at a slight angle to the long axis. Occasional elongate specimens are sausage or banana-shaped. Others have more or less symmetrically oval to lenticular outlines with the tubes originating from near the mid-line. This apparent symmetry may arise, however, because the test is being viewed from above or below rather than from the side. In a few such specimens (about 3% of the total) the outline is a broad, symmetrical oval (length:height ratio 1.85–2.50).

The protoplasm is colourless and fairly homogenous with no obvious exotic inclusions. It occupies most of the test interior. At either end of the test the protoplasm is usually interrupted by tubular invaginations which appear to be extensions of the lumens of the apertural tubes into the protoplasm. These structures are probably some form of endosolon (*sensu* Knight 1986). A fine thread of protoplasm sometimes extends along the axis of the endosolon into the apertural tube. In 9.5% of specimens, the protoplasm is divided into two (in one case three) sections by a more or less obvious constriction which is also reflected in the test wall. There is usually (about 90% of specimens) a single, large, centrally located nucleus, 8–32μm in diameter (usually 10–19μm, mean 16 ± 4μm, 202 observations). A few specimens (about 3%) appear to be multinucleate, their protoplasm containing up to 11 or 12 smaller (4–5μm), nucleus-like bodies rather than a single large nucleus.

Description. (*Challenger* material; Figs 5a–ff, 6a–jj, 7a–m, 8c, d, f, g). Specimens from the bathyal Porcupine Seabight tend to be larger, on average, than those from the abyssal BIOTRANS area (Table 1). Two rather distinct forms can be recognised in this material. In form A the apertural tubes are weakly developed, usually forming only slight extensions (3–10μm long) at either end of the test. The shape of the test is broadly similar to that of the BIOTRANS specimens. It is elongate, tapers towards both ends, and usually has an approximately lenticular lateral outline with one side being convex and the other straighter and sometimes slightly concave. Overall, the test is often gently curved. The apertures are located to one side of the mid-line. However, in a few cases, the test is more symmetrical in outline with the line joining the apertures passing close to the mid-point.

In form B, the apertural tubes are clearly developed structures, 8–27μm long (mean 18.0 ± 4.3μm, n = 66) and 5–19μm wide (mean 9.9 ± 3.5, n = 64). The lateral outline resembles that of form A, although it tends to be more oval and symmetrical, with the tubes located closer to

Table 1 *Tinogullmia riemanni*; dimensions of specimens from *Meteor* and *Challenger* samples

	Range (μm)	Mean ± S.D. (μm)	Number of measurements
Meteor material:			
Length including tubes (L1)	44–248	114.4 ± 35.0	268
Length excluding tubes (L2)	39–235	106.7 ± 33.9	261
Width (W)	13–96	35.6 ± 12.2	271
L2 : W ratio	1.85–4.81	3.03 ± 0.49	260
Challenger material (Form A):			
Length including tubes (L1)	110–285	181.2 ± 39.1	73
Length excluding tubes (L2)	116–282	173.5 ± 40.7	29
Width (W)	25–101	57.6 ± 12.7	73
L2 : W ratio	1.83–4.37	3.14 ± 0.56	45
Challenger material (Form B):			
Length including tubes (L1)	98–318	173.0 ± 47.6	37
Length excluding tubes (L2)	82–294	140.9 ± 43.4	38
Width (W)	34.4–93.0	55.0 ± 13.0	38
L2 : W ratio	1.87–3.21*	2.47 ± 0.37*	37

* excludes one elongate specimen with L2 : W ratio = 5.3

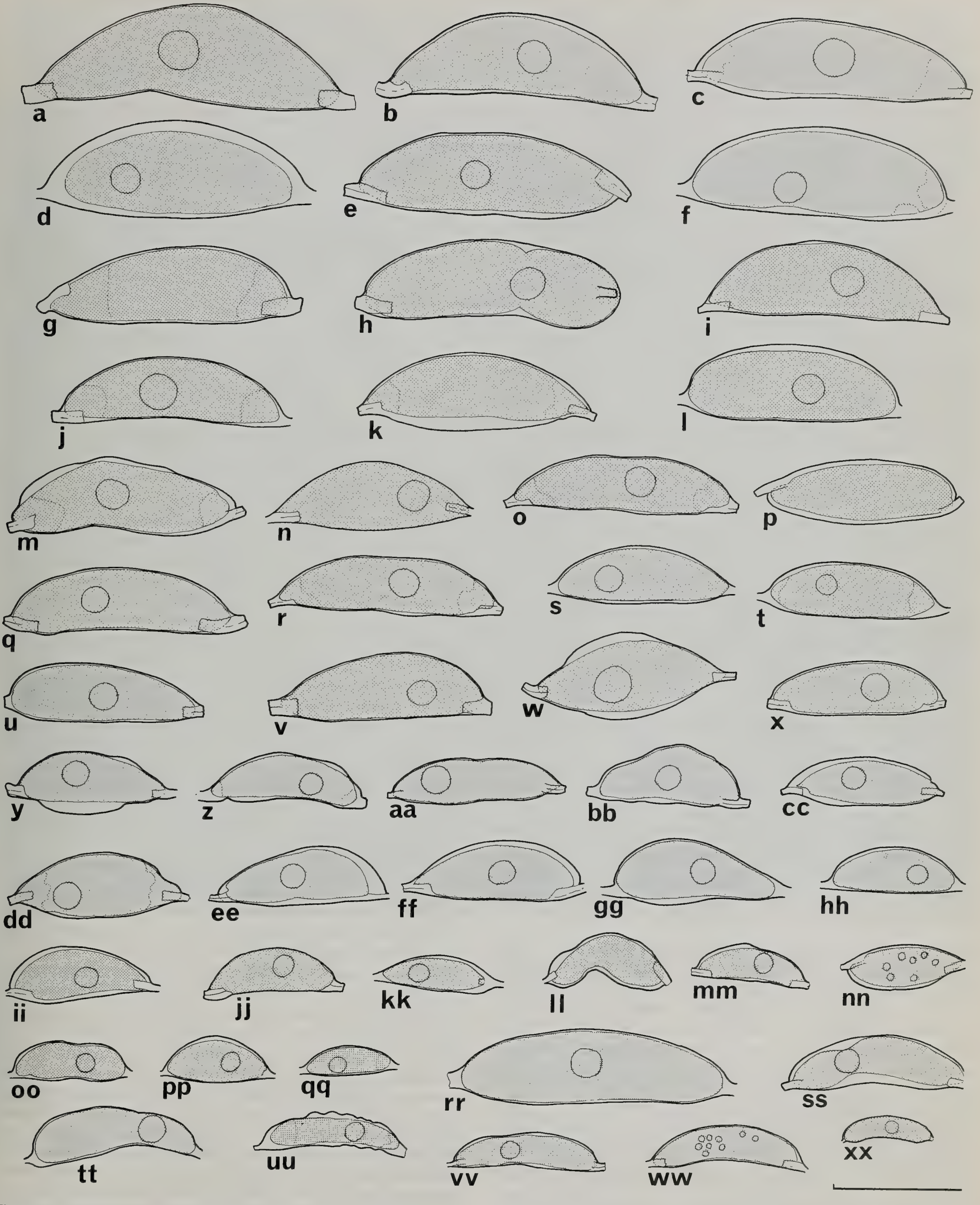
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Fig. 1 *Tinogullmia riemanni* sp. nov. Specimens from BIOTRANS phytodetritus samples. Holotype (a). Other specimens are from Stns 172 (s, hh, oo, pp, rr, ww, xx); 179 (a–e, g, h, m, o–r, u, w, x, z–bb, dd–gg, ii–jj, mm, nn, qq, tt, uu); 200 (j, l, n, t, v, y, cc, kk, ll, vv). Specimens from BIOTRANS sediment samples: Stn 179 (f, i, k, ss). The holotype is deposited under SMF 1086. Other specimens are deposited under SMF 1086 (c, e, u, w, jj); ZF4783–4786 (h, m, o, r); ZF4794–4795 (k, ss). The remaining specimens are unregistered. Scale bar = 100μm.

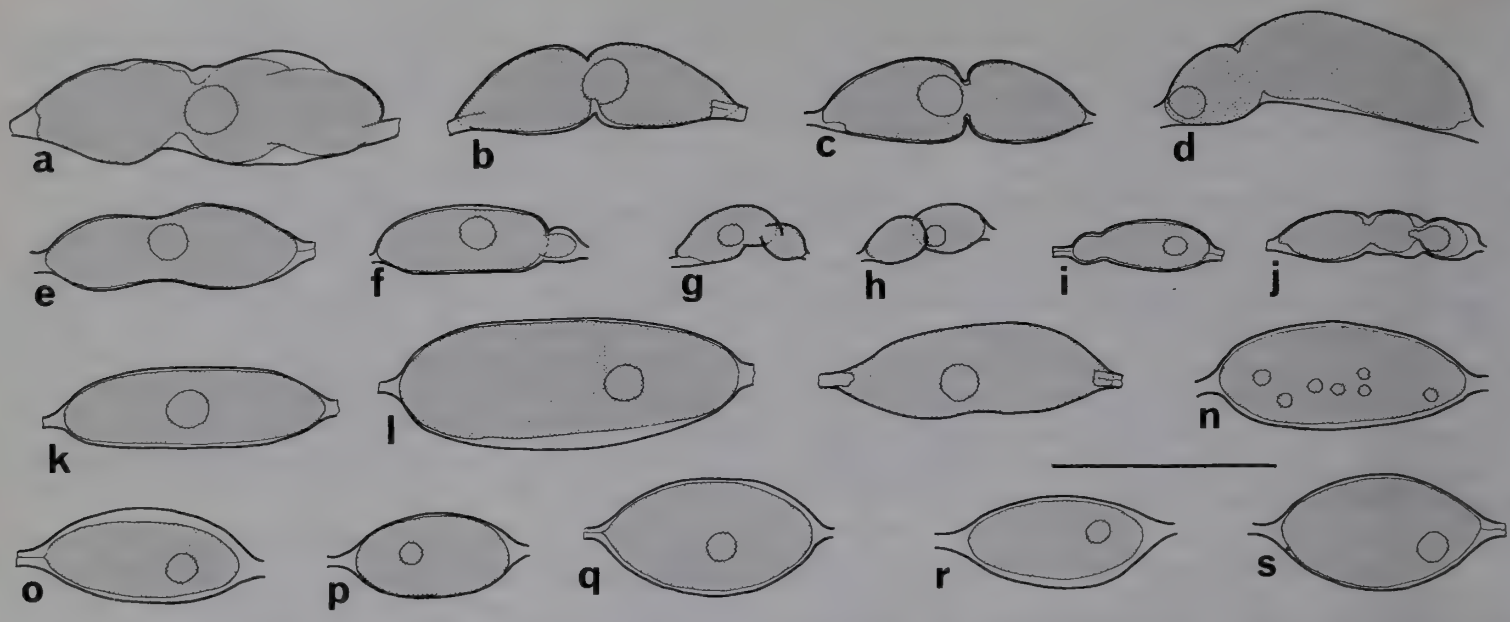

Fig. 2 *Tinogullmia riemanni* sp. nov. Specimens from BIOTRANS phytodetritus samples: Stn 172 (c, f, n); 179 (b, e, g, i, k, l, s); 200 (a, d, h, j, l). Specimens from BIOTRANS sediment samples: Stn 179 (o–r). Specimens are deposited under SMF 1086 (b); ZF4796–4799 (o, p, q, r). The remaining specimens are unregistered. Scale bar = 100μm.

the midline. The tubes themselves are often directed at a slight angle to the mid-line. One usually elongate specimen (length:width ratio = 5.3) has an almost cylindrical test (Fig. 6i).

In both forms, the larger and more regular shaped specimens have approximately circular cross-sections or are slightly flattened. Smaller specimens may be more clearly flattened and the degree of flattening sometimes varies along the length of the specimen. Overall, the thickness of the test ranges from 60% to 100% of the width.

An endosolon is sometimes developed in both forms. As in the BIOTRANS material, the protoplasm may be divided into two or three sections by constrictions which are also reflected in the test wall. The thickness of the protoplasm may vary also, with some areas being thicker than others. In form B, the protoplasm is separated from the test wall by a distinct space of narrow but uniform width. Also, a fine thread of protoplasm extends along the axis of the tube. About 90% of specimens have a single nucleus 10–26μm in diameter (mean 17.4 ± 3.3). Some of the remaining specimens have a number of smaller nuclei.

REMARKS. The two forms in the Porcupine Seabight material differ from each other mainly in the degree of development of the apertural tubes. Compared with specimens from the type locality, both forms are somewhat larger and sometimes slightly flattened rather than circular in cross section. The apertural tubes are also more strongly developed in form B than in the BIOTRANS specimens. These differences are relatively minor, particularly considering the notorious morphological variability of allogromiins (Arnold 1954, Grell 1988, Hedley *et al.*, 1968, Schwab 1977, Siddal 1880). There is little doubt that the Procupine Seabight specimens, and those from the type locality, together constitute a single species.

The elongate test with terminal apertures places this species clearly within the Shepheardellinae, as defined by Loeblich & Tappan (1988, p. 15). This subfamily includes four genera: *Nemogullmia* Nyholm 1953, *Phainogullmia* Nyholm 1955, *Shepheardella* Siddal 1880, and *Tinogullmia* Nyholm 1954, all of which are extant. The new species most closely resembles *Tinogullmia* in general test morphology, the development of terminal apertural tubes, the presence of a single nucleus, and the relatively homogenous protoplasm free from detrital particles and other exotic inclusions. *Nemogullmia* and *Shepheardella* are both much larger (1–19mm) and more elongate (often thread-like), while *Phainogullmia* has an opaque, yellowish-brown test wall composed of superimposed lamellae.

Tinogullmia hyalina Nyholm 1954, the type species of this hitherto monotypic genus, has not been reported since it was first described from 30–70m depth in the Gullmar Fjord, Sweden (Nyholm 1954). The apertural tubes of *T. hyalina* closely resemble those developed in *T. riemanni* form B from Stn 51615. However, *T. hyalina* differs from the new species in several respects. It is much larger (1.1–1.3mm), more elongate, tubular in shape, and sometimes has a large, centrally located vacuole. *Tinogullmia reimanni* usually lacks a vacuole, although a bubble-like cytoplasmic structure, resembling the central vacuole of *T. hyalina*, is clearly visible near one end of the protoplasmic mass in two specimens of *T. riemanni* from Stn 51615 (Fig. 8c).

The new species usually has a single, large, clearly visible nucleus. However, a number of smaller nuclei are present in a few specimens. In some species of primitive, monothalamous foraminifera, nuclear polymorphism is a feature of the life-cycle, the uninucleate specimens being gamonts (which reproduce sexually) and the multinucleate specimens being agamonts (which reproduce asexually) (Goldstein 1988). Some elongate allogromiins, for example *Nemogullmia longivariabilis* Nyholm 1953 and *Cylindrogullmia alba* Nyholm 1974, undergo 'serial budding' during which incipient new individuals are delimited by constrictions of the protoplasm and test. Rather similar test constrictions occur in some specimens of *T. riemanni*. However, constricted individuals never have more than one nucleus and therefore seem unlikely to be undergoing budding. Constrictions unrelated to reproduction have been observed in *Phainogullmia aurata* Nyholm 1955.

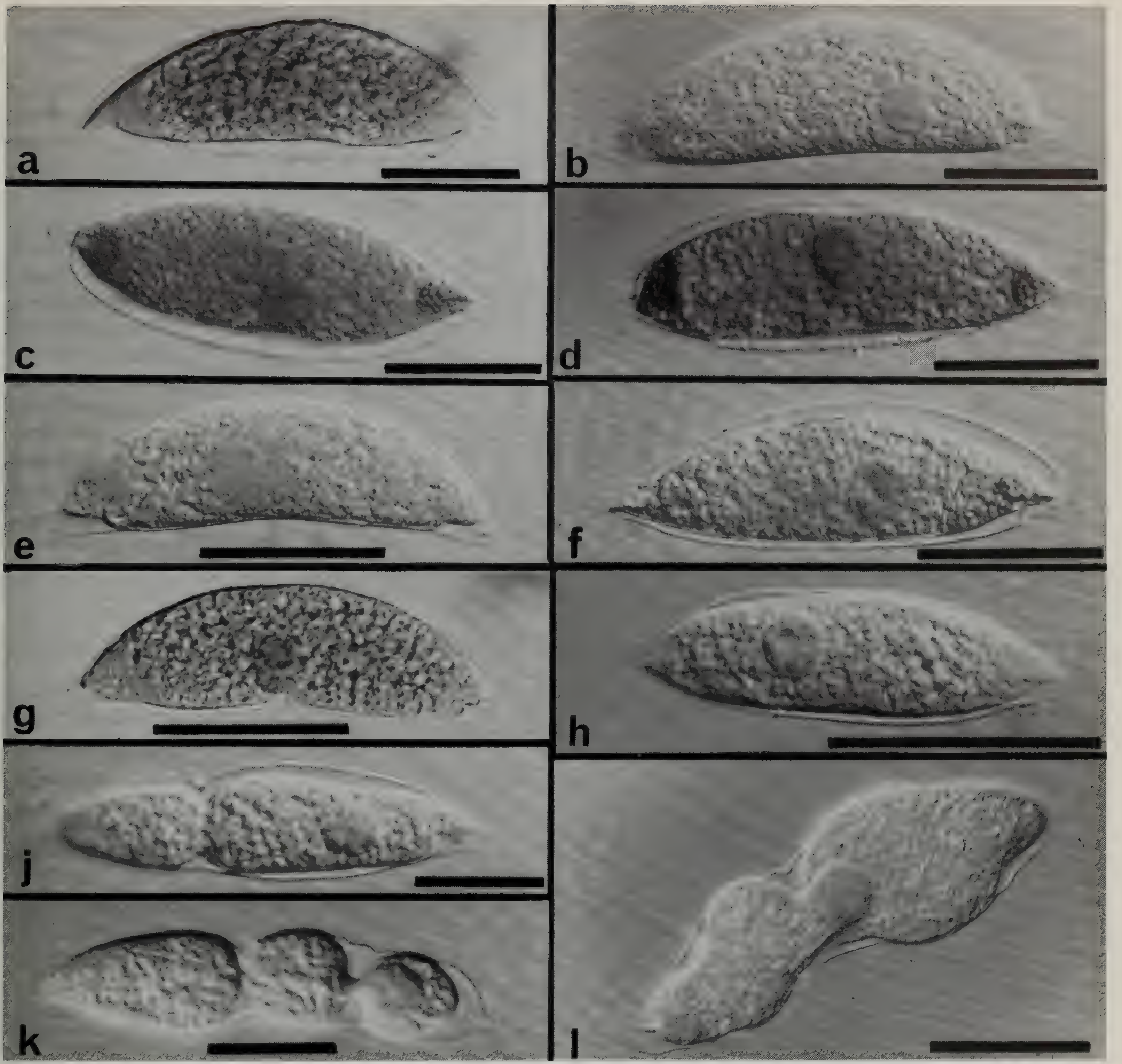

Fig. 3 *Tinogullmia riemanni* sp. nov. Specimens from BIOTRANS phytodetritus samples: Stns 179 (a, g); 200 (b, e, h, i, j, k). Specimens from BIOTRANS sediment samples: Stn 200 (c, d, f). Scale bars: a–h, k = 50μm; i, j = 25μm. All photographs taken using Nomarski interference contrast.

ECOLOGY

In the multiple corer samples collected in the BIOTRANS area, the sediment surface was sometimes overlain by brownish-green phytodetritus, either as a more or less complete layer, or as isolated aggregates (Gooday 1988*a*, Lochte & Turley 1988; Thiel *et al.*, in press). This material was first described from the Porcupine Seabight (Billett *et al.*, 1983, Lampitt 1985, Rice *et al.*, 1986). It consists of phytoplankton, and other organic remains, bound together into gelatinous masses which settle rapidly (100–150m per day) to the sea-floor following the spring bloom. Most specimens (93.7%) of *Tinogullmia riemanni* from this site were found embedded in the phytodetritus and only a few (6.3%) occurred in the underlying sediment (Gooday 1988*a*). This was the most abundant species in the phytodetritus assemblages, making up 41.8% of all foraminiferal inhabitants, almost twice as many as the second ranked species *Alabaminella weddellensis* (Earland) (21.2%).

Multiple corer samples were collected during April (Stn

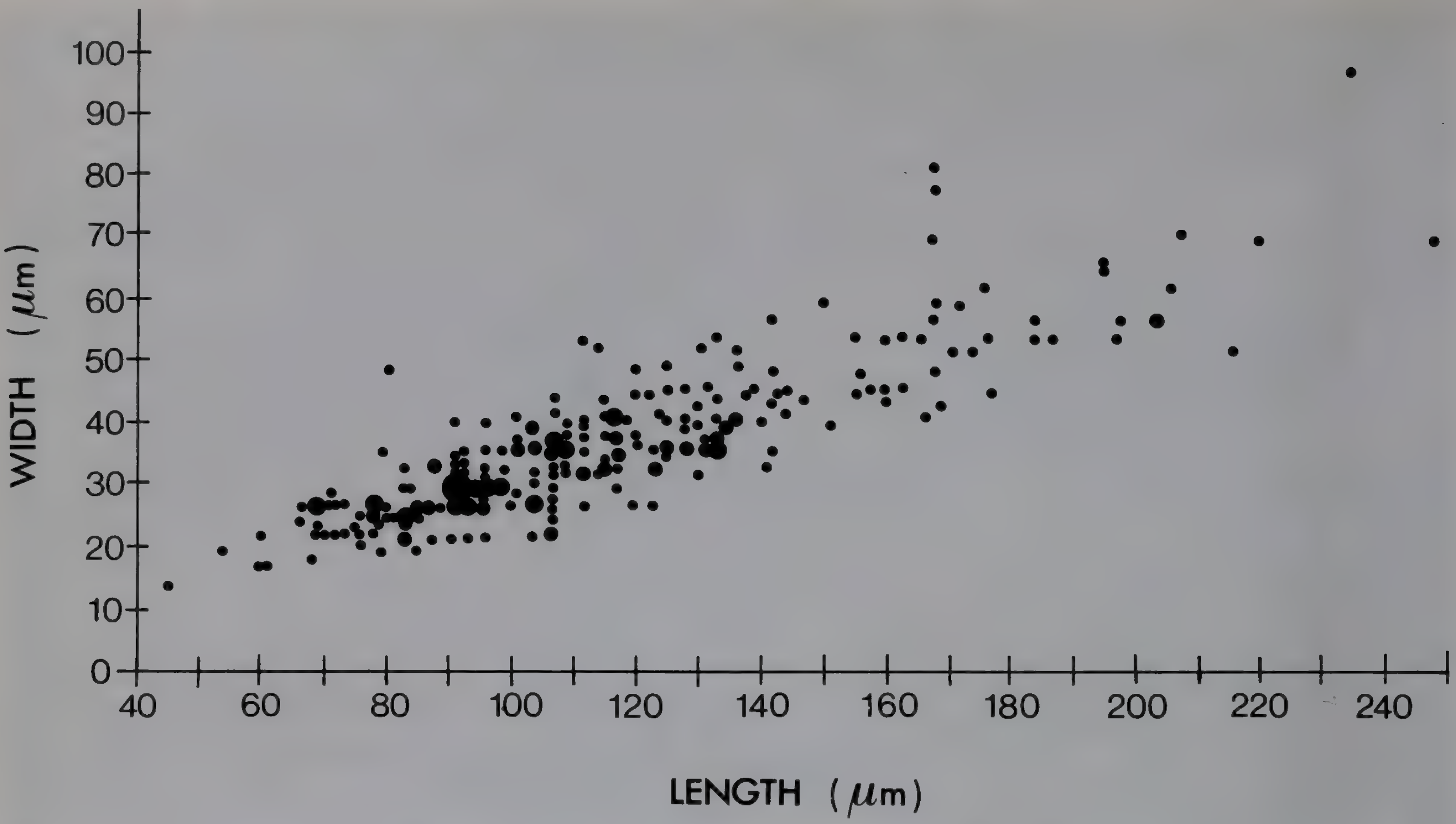

Fig. 4 *Tinogullmia riemanni* sp. nov. Plot of test length (including terminal tubes) against width for 250 specimens from BIOTRANS samples.

51502) and July (Stn 51615) at the Porcupine Seabight site. Phytodetritus was present during July but not during April. In the April sediment samples *T. riemanni* occurred only very occasionally. When sorting sediment subsamples from the July cores, aggregates of phytodetritus were separated from the sieve residues and examined separately for living inhabitants. More than three quarters (78%) of the 171 specimens of *T. riemanni* originating from Stn 51615 were found in the sediment assemblage, where the new species made up 3.13% of the total foraminiferal population and was ranked seventh in abundance (Gooday & Lambshead 1989). Thus, it was significantly more abundant in sediments overlain by phytodetritus than in sediments collected in the same area, earlier in the year, before the deposition of phytodetritus. Only 22% of *T. riemanni* specimens occurred within the phytodetritus. Included among these were a few specimens found within empty copepod moults which probably originated from the detrital aggregates (Fig. 8f, g). It is not clear why the proportion of detritus inhabiting specimens should be lower at this bathyal site than in the much deeper BIOTRANS samples. However, one possible explanation is that specimens were washed out from the detritus into the sediment during the storage and sieving of samples (Gooday and Lambshead 1989).

Recently (September 1989), *T. riemanni* has been discovered in phytodetrital samples collected from the Porcupine Abyssal Plain (48° 50′N, 16° 30′W, 4810m), midway between the Porcupine Seabight and the BIOTRANS area.

Gooday (1986*b*) has reviewed the sparse literature on deep-sea allogromiins. The abundance of these foraminifera in a box core recovered from 7298m in the Aleutian Trench (Jumars & Hessler 1976) may reflect the high food supply to this region. A connection with organic material is also suggested by Wolff's (1979*a*, 1979*b*) report of three allogromiins attached to the inner wall of a *Thalassia* rhizome from 2288m in the northwest Atlantic off Georgia. Such a relationship would be consistent with observations on the habitat preferences of shallower water allogromiins. Most information is available from the Gullmar Fjord and Skagerak where a diversity of such foraminifera thrive on the uppermost detrital layers of soft, muddy sediments at depths of a few tens to a few hundreds of metres (Nyholm 1953, 1954, 1955, 1957, Nyholm & Gertz 1973). An unnamed allogromiin is the second most abundant foraminiferal species living in an intertidal mudflat (presumably rich in organic material) near the mouth of the river Tamar, southwest England (Ellison 1984).

ACKNOWLEDGEMENTS. I thank Prof. H. Thiel for inviting me to participate in *Meteor* Cruise 3, Dr M. V. Angel, Mr M. H. Thurston and Dr J. Whittaker for critically reading the manuscript, and Mr M. Conquer for his careful photographic printing. This is BIOTRANS publication no. 18.

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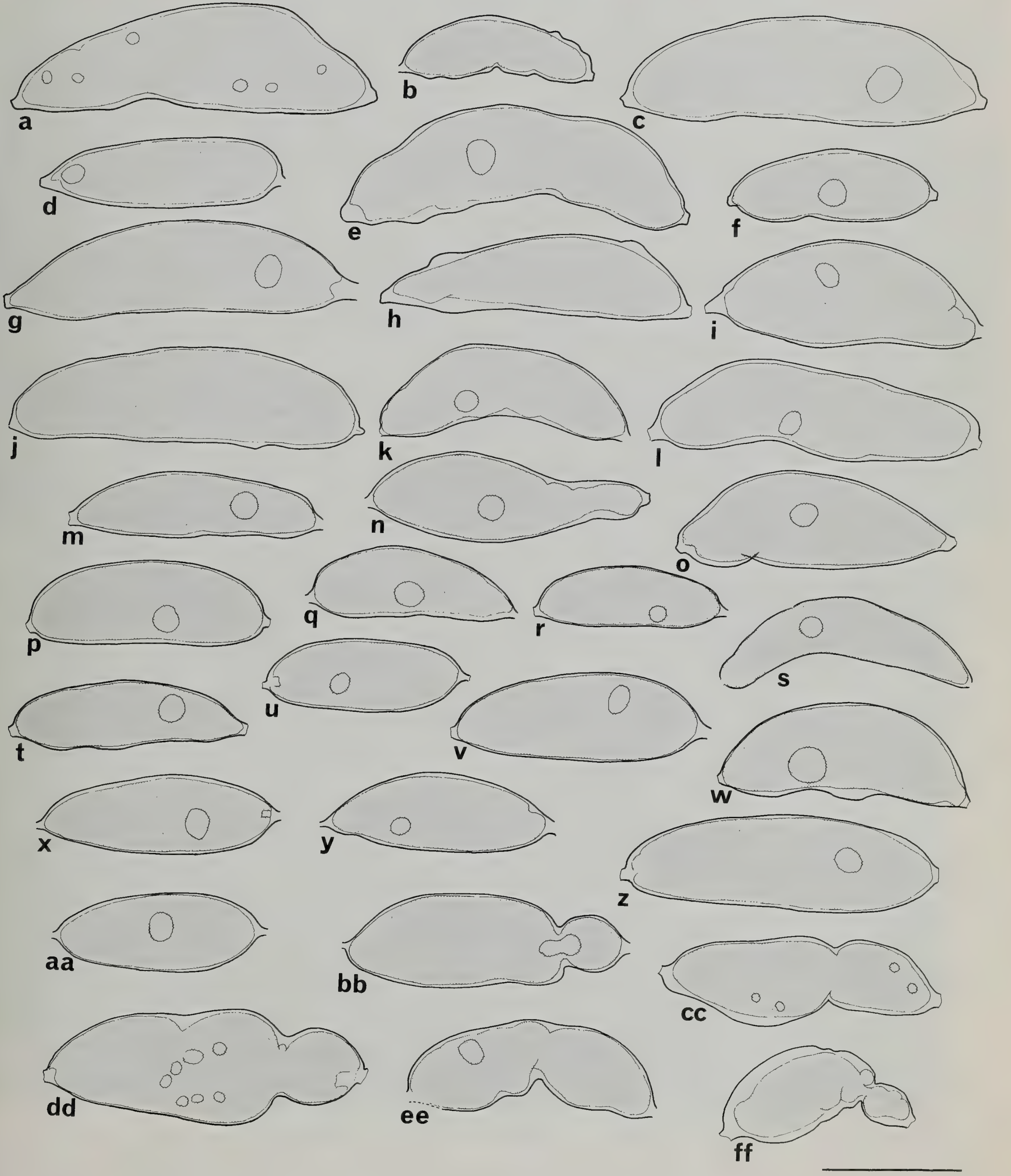
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Fig. 5 *Tinogullmia riemanni* sp. nov. Specimens of form A from Stn 51615, Porcupine Seabight: samples 51615/1A (a, c, d, l, m, aa, cc); 51615/1B (e, g, k, n, o, p, r, v, w); 51615/5B (h, i, u, y); 51615/5C (b, j, s, x, z, ff); 51615/5D (f, q, t, bb, dd, ee). Scale bar = 100µm.

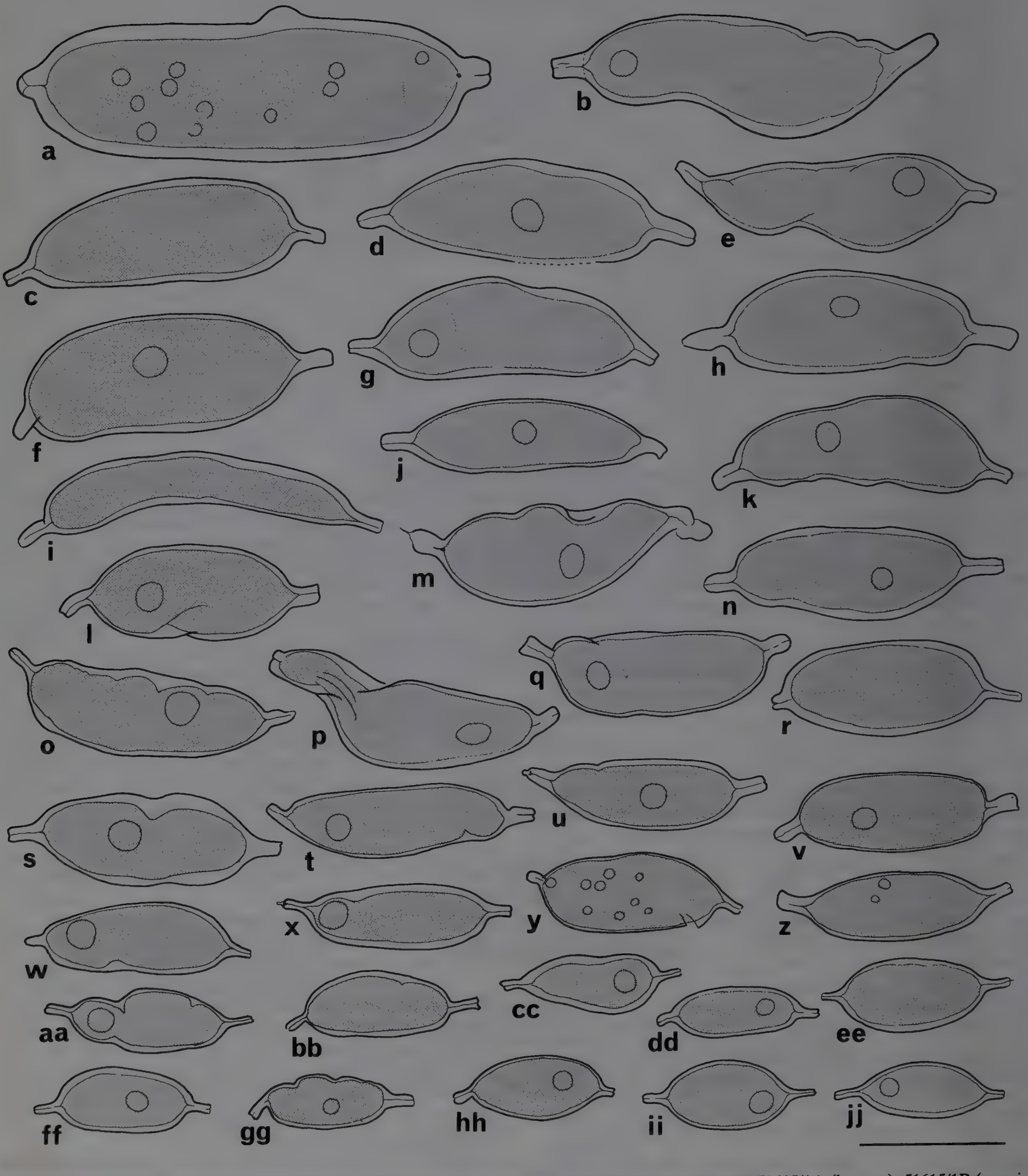
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Fig. 6 *Tinogullmia riemanni* sp. nov. Specimens of form B from Stn 51615, Porcupine Seabight: samples 51615/1A (b, t, gg); 51615/1B (e–g, j, l, s, w, x, z, aa, jj); 51615/5B (i); 51615/5C (a, c); 51615/5D (d, h, n, p, q, u, v, bb–ff, hh, ii); 51615/6A (r); 51615/6B (k, m, o, y).

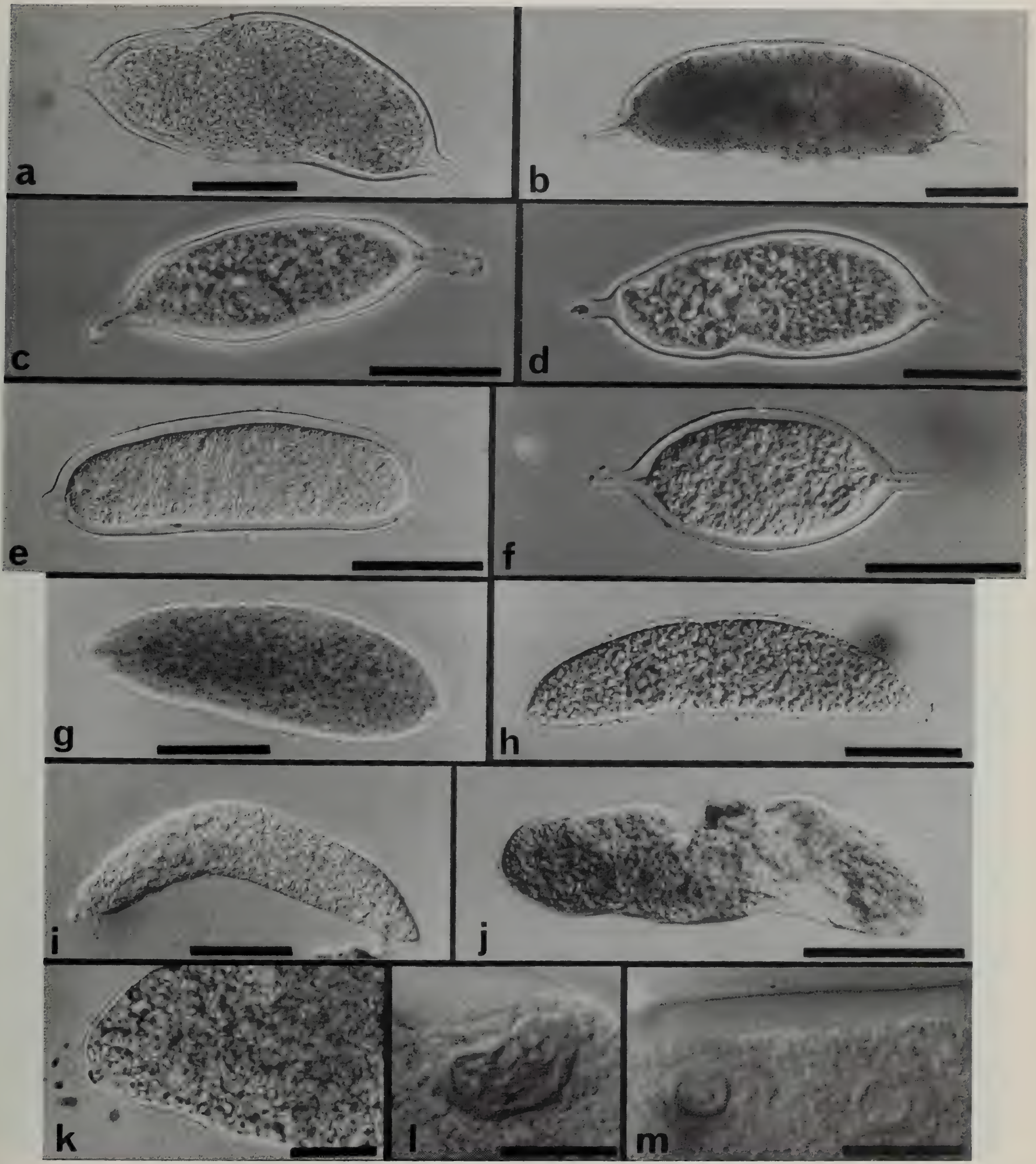

Fig. 7 *Tinogullmia riemanni* sp. nov. Specimens from Stn 51615, Porcupine Seabight. Form B, sample 51615/1B (a, c, d); form B, sample 51615/5D (b, f); form B, sample 51615/5C (e); form A, sample 51615/1B (g); form A, sample 51615/1A (h); form A, sample 51615/5C (i); form A, sample 51615/4D (j); form A, sample 51615/4D, end of test with apertural tube (k); form A, sample 51615/4D, nucleus (l); form B, 51615/5C, nuclei of multinucleate specimen illustrated in e (m). Scales: a–d, f–i = 50μm; e, j, = 100μm; k, m = 25μm; l = 10μm. a, b, e–m taken using Nomarski interference contrast, others using phase contrast.

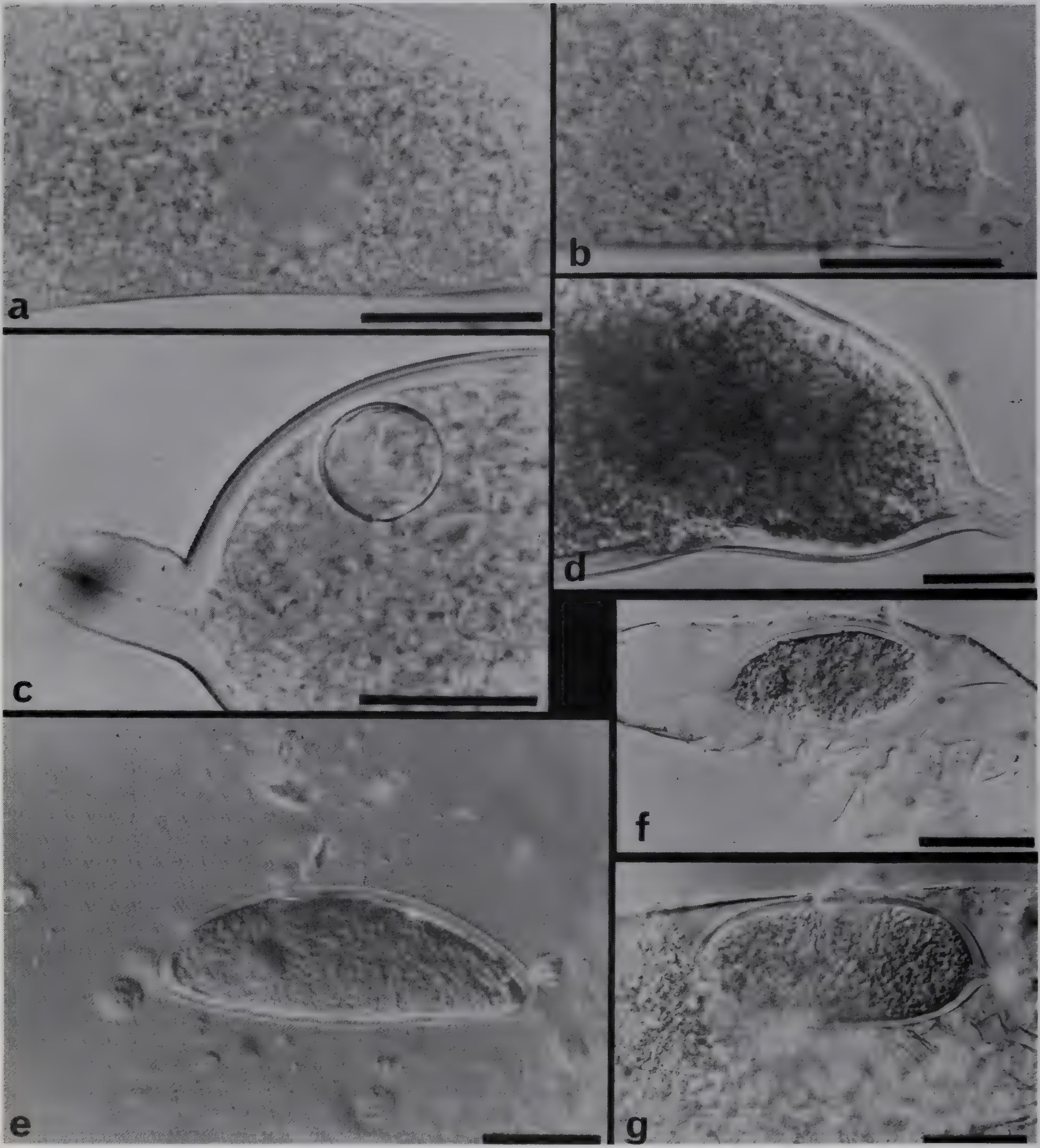

Fig. 8 *Tinogullmia riemanni* sp. nov. Specimens from BIOTRANS area (a, b, e) and Stn 51615, Porcupine Seabight (c, d, f, g). Stn 200, detail of nucleus of specimen illustrated in Fig. 3b (a); detail of apertural tube and endosolon of same specimen (b); sample 51615/1A, apertural tube and transparent, vacuole-like structure (c); sample 51615/1B, end of specimen illustrated in Fig. 7a showing apertural tube (d); Stn 200, specimen embedded in phytodetritus; the sphaerical structures are 'minipellets' produced by phaeodarian radiolarians (e); sample 51615/5D, specimens inside empty copepod moults (f, g). Scales: a–d = 25µm; e–g = 50µm. All photographs were taken using Nomarski interference contrast.

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Manuscript accepted for publication 18 November 1989

Bull. Br. Mus. nat. Hist (Zool.) **56**(2): 105–134 Issued 25 October 1990

Larval and post-larval development of *Anapagurus chiroacanthus* (Lilljeborg, 1855) Anomura: Paguroidea: Paguridae

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SYNOPSIS. Four zoeal, a megalopal, first and second crab stages of the hermit crab *Anapagurus chiroacanthus* are described from laboratory reared material and compared with previous brief larval accounts of this species. Present larval evidence suggests that *A. chiroacanthus* may be phylogenetically closest to *Cestopagurus* but separated on a number of apomorphic features.

INTRODUCTION

Although our knowledge of pagurid larval development has improved considerably since Gurney's (1942) evaluation of decapod larval features, it is still relatively poor when compared with the considerable amount of information now available on brachyuran ontogeny (eg see Rice, 1980; Martin, 1984). In particular, of the 20 species currently assigned to the genus *Anapagurus,* the larval development of only six has been described (Nyblade & MacLaughlin, 1975: 286), but none of these accounts is sufficiently detailed to compare satisfactorily with the more informative larval descriptions now available of other pagurid species (Dechancé, 1961; McLaughlin & Gore, 1988).

In July 1984 two ovigerous *Anapagurus chiroacanthus* (obtained off Millport, Isle of Cumbrae, Scotland by staff of the Bryozoa Section of this Museum) were donated to the Crustacea Section. These crabs were maintained in the larval rearing laboratory until their eggs hatched. The larvae were reared through to second stage crab and provided material for the first detailed description of the complete larval and early post-larval development of this species.

MATERIALS AND METHODS

Each crab was kept in 500cm of gently aerated sea water until its eggs hatched. Larvae and the juvenile crabs were reared in plastic compartmented trays, each compartment containing 20cm of filtered water. The larvae were fed newly hatched *Artemia* nauplii and the crab stages finely shreaded macerated *Littorina* tissue; all were maintained at 12–15°C. Small lengths of plastic conduit were provided and eventually accepted by juvenile crabs as a shelter. Development time, from hatching to the appearance of second stage crab, took an average of 82 days.

All material was initially fixed and stored in the solution formulated by Steedman (1976: 148) and was later transferred to 70% industrial methylated spirit.

Dissected appendages were transferred to glycerol as temporary micro-slide preparations, and drawings were made using a *camera lucida* attached to an Olympus BH2–NIC microscope. Setal types were identified using interference contrast (Nomarski) and confirmed by viewing with a Hiatachi S800 field emission scanning electron microscope.

The crabs and reared material are deposited in the Collection of the Zoology Department, British Museum (Natural History), accession number: 1989: 191.

Measurements: (average measurements of 4–5 specimens) C.L. = carapace length measured from tip of rostrum to median posterior margin of carapace for larval stages. S.L. = shield length measured from rostral apex to shield posterior margin, for crab stages, T.T. = total length measured from rostral apex to posterior margin of telson.

RESULTS

Anapagurus chiroacanthus (Lilljeborg, 1855)

LARVAL REFERENCES. *Spiropagurus chiroacanthus:* Sars, 1890:155, Tab. 3 (prezoea, zoea, I, IV, megal); *Anapagurus chiroacanthus*: MacDonald et al, 1957:243, fig. 10 (zoeae I–IV, megal); Pike & Williamson, 1959:3, figs 34–38, 53 (zoeae I–IV, megal); Pike & Williamson, 1960:525, fig 8E (zoea I).

Zoea I.

C.L. 1.0mm., T.L. 2.10mm.

CARAPACE (Fig. 1a). Longitudinally strongly convex in lateral view. Rostrum stout reaching well beyond apex of antennule exopod and slightly more than half median length of carapace; posterio-lateral spine stout.

EYES. Well developed and partly fused to carapace.

ABDOMEN (Figs. 1a, 2a, b, 17a). 5-segmented, segment 5 longest. Posterio-dorsal margins of 1–3 with 4 (sometimes 5 on 3) minute denticles; 4,5 each with pair of stout spines. Posterio-lateral margins of 2,3 each with 2 denticles; 4,5 each with spine and sometimes pair of small lateral simple setae.

TELSON (Figs. 2a, 16a). Slightly broader than long, measured from base of short cuspidate/spiniform* furcal setae. Posterior margin convex with single row of large denticulettes and armed with 5 plumodenticulate setae on each half and an outermost small pappose seta; second innermost plumodenticulate seta longest and fifth shortest.

ANTENNULE (Fig. 1b). Exopod sub-cylindrical, with 1 sub-terminal plumose seta, 2 short and 1 long terminal aesthetasc.

ANTENNA (Figs. 1c, 17b). Protopod with stout denticulate medio-distal spine. Exopod broad (maximum width about half length), with long denticulate stout disto-external spine measuring about half exopod length; exopod with 9 marginal plumose setae (innermost short and stout) and 1 simple seta next to disto-external spine. Endopod shorter than exopod (maximum width about one quarter of length), narrowing slightly distally and with 2 terminal plumose setae.

MANDIBLES (Fig. 1d). Well developed, incisor differentiated from molar process, both mandibles of similar shape.

MAXILLULE (Fig. 1e). Exopod 3-segmented, terminal segment longest, with 1,1,2 plumodenticulate setae, short on segment 1. Basis distally narrowed, terminating as 2 stout equally developed cuspidate setae with sockets hardly discernible and bearing 4–7 graded denticles. Coxa broad, distal margin with 5 long thin plumodenticulate setae, 2 short sub-marginal simple setae and a few short disto-internal microtrichia.

MAXILLA (Figs. 1f, 18a). Scaphognathite lobe developed anteriorly only and with 5 short marginal plumose setae. Endopod 'stepped' ie with broad outer and much smaller inner lobe bearing 3,3 plumodenticulate setae. Basis bilobed, each with small distal process and 4,4 setae (3 plumodenticulate and one innermost simple on each lobe), outer margin of endite with few microtrichia. Coxa bilobed with 2,7 plumodenticulate setae, inner margin of endite with few microtrichia.

MAXILLIPED 1 (Figs. 2c, 18b, c). Basis with 1–1–3–3 plumodenticulate setae on inner margin. Endopod 5-segmented with 3,2,1,2,4+1 plumodenticulate setae, all except last arising from inner distal margins; outer distal margins of segments 2–4 with microtrichia; setules investing plumodenticulate setae on segment 5 varying from hardly discernible to stout and long (see pl. 3c). Exopod incipiently divided medially and with 4 long distal plumose setae.

MAXILLIPED 2 (Fig. 2d). Basis with 1 stout plumodenticulate and 1 simple seta on inner distal margin. Endopod 4-segmented, with 2,2,2,4+1 setae; setae on inner margins of segments 2–4 represented by at least two distinct plumodenticulate types (see inset to figure); microtrichia on outer margins of segments 2,3. Exopod incipiently divided medially and with 4 distal long plumose setae.

MAXILLIPED 3 (Fig. 2e). With incipiently developed basis and exopod.

Zoea II

C.L. 1.25mm., T.T. 2.55mm.

CARAPACE (Figs. 3a). Rostrum distally slightly curved downwards and usually not longer than half median length of carapace.

ABDOMEN (Fig. 3a, 4b, c). Posterio-dorsal margin of segment 3 with 6 (sometimes more) minute denticles. Posterio-lateral margins of segments 2,3 usually with only one small posterior denticle.

TELSON (Figs. 3k, 4a). Posterior margin with an additional innermost pair of small plumodenticulate setae (total of 7 plumodenticulate setae on each half).

EYES (Fig. 3b). Free from carapace margin; cornea very broad.

ANTENNULE (Fig. 3c). Exopod with one long stout aesthetasc and 4 thin shorter ones.

ANTENNA (Figs. 3d, 17c). Protopod with a disto-external spine. Exopod narrower (maximum width much less than half length), with 10 plumose setae; most posterior seta on inner margin of exopod much longer than in previous stage and seta next to disto-external spine plumose. Endopod basally broadened.

MANDIBLES (Fig. 3e). Molar processes relatively broadened and less noticeably differentiated from incisor portions.

MAXILULLE (Figs. 3f, g). Basis (f) with 2 additional slightly smaller spiniform setae (grading to cuspidate type) and in some specimens a minute marginal simple seta. Coxa (g) with innermost plumodenticulate seta stout.

MAXILLA (Fig. 3h–j). Scaphognathite (j) with 6–7 marginal plumose setae. Basis (h) with one additional plumodenticulate seta on inner lobe (total of 4,5). Coxa (i) with one additional ?simple seta on outer lobe (total of 3,7).

MAXILLIPED 1 (Fig. 4d). Endopod segments 1–3 each with one long plumose seta on disto-outer margin; microtrichia absent. Exopod with 7 distal plumose setae.

MAXILLIPED 2 (Fig. 4e). Endopod segments 2,3 each with one long plumose seta on disto-outer margin; microtrichia absent. Exopod with 7 distal plumose setae.

MAXILLIPED 3 (Fig. 4f). Articulation between basis and exopod incomplete. Exopod incipiently divided medially, distally with 6 plumose setae.

PLEOPODS (Fig. 4a). Posterior-ventral part of segment 6 with very incipient plepod buds.

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* Some specimens have small denticles on surfaces of these setae thus placing them into the cuspidate category. See p. 00 for terminology.

Zoea III

C.L. 1.4mm., T.T. 3.10mm.

CARAPACE (Fig. 4g). Rostrum much shorter than median carapace length.

ABDOMEN (Fig. 5a–c). Sixth segment developed. Posteriodorsal margin of segment 1 variably denticulate or unarmed. Segments 2,3 with 4–5 denticles. Segments 4,5 with additional pair of small denticles. Segment 6 unarmed. Posteriolateral margins of segments 2,3 variably denticulate as shown in b.

TELSON (Fig. 5a, d). Dorsal surface with pair of small simple setae. Furcal and plumodenticulate setae on posterior margin slightly shorter than in previous stage; second innermost plumodenticulate seta replaced by stout spine, denticulate in distal half.

ANTENNULE (Fig. 5e). Peduncle incipiently 2-segmented; small disto-external simple seta present and more or less medially placed longer plumodenticulate seta. Exopod with 6 aesthetascs. Endopod developed as conspicuous bud partly sutured from peduncle and with one proximal plumodenticulate seta, one apically placed plumose seta and one aesthetasc.

ANTENNA (Fig. 5f). Endopod distally acute and with only one (?)simple sub-distal seta present.

MANDIBLES (Fig. 4h). Incisor region broader and with a more complex dentition.

MAXILLULE. Setation and shape unchanged.

MAXILLA (Fig. 5g). Scaphognathite with 9 marginal plumose setae; setation of other endites unchanged.

MAXILLIPED 1. Setation of endites unchanged.

MAXILLIPED 3. (Fig. 5h). Exopod with 7 plumose setae. Endopod present as conspicuous bud almost as long as basis.

PEREIOPODS (Fig. 4g). 1–4 developed as incipient buds.

PLEOPODS (Fig. 5a). Exopod of uropod well developed, almost as long as telson, thin, tapering distally into acute process invested with small denticulettes, inner margin with 6 long plumose setae.

Zoea IV

C.L. 1.82mm., T.T. 3.85mm.

CARAPACE (Fig. 6a). Posterio-lateral spine much smaller than in previous stages.

ABDOMEN (Fig. 7a–c). Posterior-dorsal margins of segments variably denticulate but segment 5 usually with additional pair of small denticles. Segments 1–5 each with a pair of dorso-median simple setae. Denticulation of posterio-lateral margins variable but segments 5, 6 always with small but prominent posterio-ventral spine.

TELSON (Fig. 7d). Posteriorly narrower. Innermost pair of plumodenticulate setae on posterior margin generally shorter than in previous stages. Dorsal surface with 2 pairs of median simple setae.

ANTENNULE (Fig. 6b). Peduncle usually with 2 disto-external simple setae. Exopod now with 9 aesthetascs, 2 strongly subdistally placed.

ANTENNA. Endopod equal in length or slightly longer than exopod, otherwise unchanged.

MANDIBLE (Fig. 6c). Dentition of left mandible noticeably different from right mandible.

MAXILLULE (Fig. 6d, 17d). Coxa with 2 additional plumodenticulate setae, otherwise setation unchanged.

MAXILLA (Fig. 6e, f). Scaphognathite posterior lobe developed and bearing 3 terminal, one sub-terminal and 13 anteriorly placed plumose setae (total 16 setae). Some coxal setae on inner lobe noticeably stouter than in previous stages.

MAXILLIPEDS 1, 2 (Fig. 6a). Exopods with 8 plumose setae, otherwise unchanged.

MAXILLIPED 3 (Fig. 6a). Endopod longer than in previous stage.

PEREIOPODS (Fig. 6a). 1–4 rudimentary. Pereiopod 1 (cheliped) incipiently segmented and with dactyl differentiated from distal propodus. 2 & 3 also incipiently segmented.

PLEOPODS (Fig. 7a, d, e). Developed as paired buds on segments 2, 3 (=pairs 1, 2). Pleopod 5 (uropod), exopod dorsal surface with 2–3 simple setae and with one additional distally placed simple seta on inner margin (total of 7 marginal setae). Endopod represented as a small bud bearing a distal plumose seta.

Megalopa

C.L. 1.0mm., T.T. 2.10mm.

CARAPACE (Fig. 8a, 9a). Longer than broad and subquadrate from dorsal aspect. A well developed sub-acute rostrum present. Anterior margin on either side slightly convex. Ocular acicles spinose. Surface of carapace sparsely setose at most.

ABDOMEN (Fig. 9a, 11d, e, 19a, b). Six-segmented. Segment 5 longest; margins of segments unarmed. Surfaces of segments 1, 4–5 with one, and of segment 6 with two pairs of dorsal simple setae in addition to pappose lateral setae present (as shown in Fig. 11d & 19a, b). Posterio-lateral margins of segments sub-truncate to rounded).

TELSON (Fig. 11d, 19d). Sub-oval to sub-quadrate, as broad as long or, where lateral margins are inflated (as in some specimens), slightly broader than long. Dorsal surface with 2 pairs of simple setae and one lateral pair present. Posterior margin with 8 long plumose setae.

EYES (Fig. 8a). Much longer than broad, reaching into basal segments of antenna.

ANTENNULE (Fig. 9b). Peduncle 3-segmented. Segments 1, 2 subequal. Segment 3 long and distally expanded. Outer surface of segment 1 with an oblique row of 6–7 plumose setae, lower margin with a distal lobe bearing one simple and one plumodenticulate seta, dorsal margin with 2 plumodenticulate and one simple seta (see inset to figure). Segment 2 with 2 distal simple setae. Segment 3 with 2 ventral and one dorsal simple seta. Exopod incipiently 4-segmented; only segment 4 usually clearly differentiated. Segments 2–3 respectively with a ventral group of 5 aesthetascs, 2 aesthetascs and a dorsal simple seta. Segment 4 with a proximal group of 3 aesthetascs, 4 terminal simple setae and a small spiniform seta (see inset to figure). Endopod 2-segmented; segment 1 with 2 and segment 2 with 6 setae (2 sub-distal).

ANTENNA (Fig. 9c). Peduncle 5-segmented. Segment 2 with 2 simple setae, distal inner margin armed with one stout spine and outer with 2 spines, one of which is ventrally placed. Segment 3 sub-triangular and with one simple seta. Supernumerary segment not visible. Segment 4 much shorter than 5 and with one simple seta. Segment 5 with 4 distal setae. Acicle (exopod) armed with 6 simple setae and terminating in 2 acute processes. Flagellum 10-segmented; segment 1 shortest; setal formula 0, 4, 1–2, 6, 1, 5, 0, 5, 3, 7–8.

MANDIBLES (Fig. 9d). Molar and incisor processes differentiated into two oval-shaped slightly concave structures without teeth or spines. Palp large, 3-segmented and with 1–2 small simple setae on distal part of segment 3.

MAXILLULE (Fig. 9e, f, 19c). Exopod reduced to simple lobe. Setae on basis reduced in size but increased in number and represented by 10–11 spiniform setae (fig. 19c) and 2 stout short plumodenticulate setae. Coxal setae reduced in number to 2–3 stout plumodenticulate and one simple seta.

MAXILLA (Fig. 8b–d). Scaphognathite with well developed anterior and posterior lobes and with 25 marginal plumose seta. Endopod reduced to simple lobe with one sub-apical simple seta. Basis with 8, 7 setae, many setules and denticles now reduced or absent, conveying appearance of simple setae (c). Coxa with 3, 3 plumodenticulate setae.

MAXILLIPED 1 (Fig. 8e). Coxa hardly demarcated from basis and with plumodenticulate and simple seta. Basis with small proximal spiniform seta and 4–5 simple setae on inner margin. Endopod as elongated lobe. Exopod developed as incipiently 2-segmented non-setosed lobe.

MAXILLIPED 2 (Fig. 8, f). Protopod elongated. Endopod developed as 2-segmented non-setosed lobe. Exopod 2-segmented, apex of segment 2 with 6 plumose setae.

MAXILLIPED 3 (Fig. 10a, 20a). Endopod with ischium to dactyl developed. Ischium with one plumodenticulate seta on disto-inner margin and merus with one on disto-outer margin. Carpus with transverse row of 6 plumodenticulate setae near distal margin. Propodus with 13–20 setae chiefly near inner and distal margins represented by small cuspidate and two types of plumodenticulate setae. Dactyl with 6–8 setae composed of two plumodenticulate types (p1, p2 in Fig. 20a). Exopod 2-segmented, apical part of segment 2 with 8 plumose setae.

PEREIOPODS 1 (CHELIPEDS) (Fig. 10b–e). Left cheliped (b, c) all segments clearly differentiated. Merus long, longitudinally sub-triangular and with one distal spine on both inner and outer margins. Carpus short, sub-triangular and with 3 spines on outer margin. Propodus and dactyl slightly compressed. Upper margin of propodal prolongation with number of spines, as shown in inset to (c). Lower margin of dactyl with at least 5 spiniform setae. Cheliped segments invested with simple and plumodenticulate setae disposed as shown in figures. Right cheliped (d, e), merus sub-triangular, with small spine on upper distal inner margin. Carpus sub-triangular with 2 small spines on upper margin. Propodus and dactyl somewhat compressed. Upper margin of propodal palm with 2 small spines, lower with several small irregular teeth or spines. Upper margin of propodal prolongation and lower margin of dactyl somewhat cristate and bearing several iregularly shaped teeth as shown in inset to (e). Cheliped segments with plumodenticulate and some simple setae (e, d).

PEREIOPOD 2 (Fig. 10f, 20b, c). Long and relatively stout, all segments clearly differentiated. Length of ischium slightly less than half length of merus. Dactyl almost as long as combined lengths of propodus and carpus. Merus and propodus with a conspicuous spine on lower distal margin. Ischium to propodus invested only with simple setae. Dactyl with simple and pappose setae (Fig. 20b, c).

PEREIOPOD 3 (Fig. 11a). Long and relatively stout; all segments clearly differentiated. Ischium greater than half length of merus. Dactyl almost as long as combined lengths of propodus and carpus. Upper distal margin of carpus and lower distal margin of propodus with spine. Ischium to propodus invested only with simple setae. Dactyl with simple and pappose setae.

PEREIOPOD 4 (Fig. 11b). Short and robust; all segments differentiated. Propodal outer surface with 5 pseudochaetal type setae. Segments invested with only plumodenticulate setae distributed as shown.

PEREIOPOD 5 (Fig. 11c, 20d). Short and robust; all segments clearly differentiated. Propodal distal outer surface with *circa* 8 pseudochaetal type setae and one on dactyl. Segments invested with plumodenticulate setae of various lengths.

PLEOPODS (Fig. 11d, e, f–j). Only pleopods 1–3 and 5 fully developed. Pleopods 4 represented as pair of buds. Pleopods 1, 2 with long protopod (h, i). Exopod short, bearing 8 long plumose setae. Endopod small, with two distal cincinnuli on inner distal margins. Pleopod 3 (j) exopod with 4 distal plumose setae; endopod absent. Outer margins of protopod and exopod with microtrichia. Pleopods 5 (uropods) of equal size. Exopod with *circa* 9 pseudochaetal type setae on outer distal part, 10 plumose and 5 plumodenticulate setae. Endopod small, with 3 pseudochaetal type setae, one proximal simple and one distal plumodenticulate seta.

GILLS (Fig. 12a). Origin of gills difficult to resolve, but at least 6 on each side in megalopa; all appear to be arthrobranchs.

Crab I

Shield length 0.56mm.

CARAPACE (Fig. 12b). Anterior margin of shield convex. Lateral projections obtuse. Ocular acicles swollen medially and distally acute. Ocular extension broad.

ABDOMEN (Fig. 15a). Segmentation indistinct and with slight increase in numbers of setae.

TELSON (Fig. 15a, d). Subquadrate. Posterior margin strongly concave, irregularly dentate and with one pair of simple setae. Dorsal surface with 5 pairs of simple setae.

EYES (Fig. 12b). Length slightly more than maximum width (measured from base of peduncle).

ANTENNULE (Fig. 12c). Peduncle 3-segmented. Segment 3 not distally expanded. Outer surface of segment 1 with oblique row of 7 or more plumose setae, lower margin with broad distal lobe bearing plumose seta and well developed spine. Segment 2 shortest. Segment 3 with 2 dorsal plumose setae but still with 2 ventrally placed simple setae. Exopod 5-segmented with 0, 6, 5, 3 aesthetascs on segments 1–4 and 3 simple distal setae on segment 5. Endopod unchanged but distal spiniform seta on segment 2 no longer present.

Antenna (Fig. 12b, e). Peduncle now 6-segmented. Segment 1 with 3 very small plumose setae on inner margin and a small spine on outer margin. Segment 2 with 7 simple setae, outer distal margin with the more dorsally placed distal spine reduced to an obtuse process. Segment 3 with one distal simple seta but with dorsally placed innermost distal obtuse process. Supernumary segment visible and intercalated below base of acicle. Apex of acicle terminating as acute process armed with average of 5 simple setae. Flagellum with 11 segments and a setal formula of 0, 0, 3, 2, 5, 1, 5, 1, 6, 4, 7–8.

Mandibles (Fig. 12f). Molar part differentiated as a transverse obtuse lobe. Incisor part forming broad slightly concave plate-like expansion. Outer distal part of protopod with prominent simple seta. Segment 1 of palp indistinctly sutured from protopod. Segment 3 with 8 cuspidate setae and one plumodenticulate type on distal margin.

Maxillule (Fig. 12g). Protopod with outer stout plumodenticulate seta without or with very few setules; outer margin of protopod with a lamellar expansion bearing marginal microtrichia. Exopod with long simple seta on inner apical margin. Basis with average of 13 cuspidate and 2 stout plumodenticulate seta (total of 15, see inset to figure). Coxa with total of 16 setae, at least 10 cuspidate type and others plumodenticulate, some probably grading from one form to the other (see figure inset).

Maxilla (Fig. 13a). Scaphognathite with average of 20 marginal plumose setae, 5 posterior setae still noticeably separated from others. Sub-apical seta on endopod represented as plumose type. Basis with 10, 10 plumodenticulate setae, many with setules and denticles very reduced or absent (see uppermost inset). Coxal outer lobe with 6 marginal and one submarginal plumodenticulate seta; inner lobe with 7 marginal plumodenticulate and a row of 13 sub-marginal plumose setae, proximal margin also with microtrichia.

Maxilliped 1 (Fig. 13b, c). Coxa differentiated from basis with average of 5–7 plumodenticulate setae. Basis with 20 setae, cuspidate grading into plumodenticulate, as shown in (c). Endopod with one plumodenticulate seta. Exopod well developed, clearly 2-segmented, one outer proximal plumose seta and one inner medial simple seta on segment 1; distal margin of segment 2 with 6 plumose setae.

Maxilliped 2 (Fig. 13d, 14a). Endopod developed and segments clearly differentiated, except basis/ischium. Coxa expanded and with 6 setae. Basis with 3 setae on inner margin. Ischium with 2, merus and carpus one, propodus 6 and dactyl with 5 setae, all plumodenticulate types (Fig. 14a). Exopod long and thin. Segment 1 with outer medial simple seta. Segment 2 still with 6 terminal plumose setae.

Maxilliped 3 (Fig. 14b). Endopod-ischium with 6 plumodenticulate setae on or near inner margin and a distal cuspidate seta. *Crista dentata* developed and composed of 5 spines; accessory tooth incipient. Merus to dactyl with setae; average setal counts respectively 5, 5, 16, 9 for these segments, of plumodenticulate type (see inset). Exopod segment 1 with 2 simple setae and one plumodenticulate seta. Segment 2 with average of 7 plumose setae.

Pereiopods 1 (Fig. 14c, d). Left cheliped (d) general proportions and spine investment unchanged except for upper margin of propodal prolongation and lower margin of dactyl, both with numerous spiniform setae. Right cheliped (c), propodal palm broad, upper and lower margins noticeably convex. Upper margin of propodal prolongation and lower dactyl margin cut into broad irregular teeth and with spiniform setae disposed as shown in inset to figure.

Pereiopods 2, 3. Unchanged except for slight changes in relative lengths of some segments and their setation.

Pereiopod 4 (Fig. 14e). Unchanged except for shape and slight increase in number of pseudochaetae on propodus.

Pereiopod 5. Unchanged except for slight increase in number of propodal pseudochaetae.

Pleopods (Fig. 14g, f, 15a–c). Pleopod 4 (g) developed. Pleopods without endopod. Numbers of plumose setae on exopod segment 2 slightly variable. Average of 8 on 1–3 and 5 on 4. Pleopod 5 (uropods), left (b) larger than right (c). Plumose setae on exopods of uropods virtually absent; numbers of pseudochaetae increased by one or 2 at most.

Crab II

Shield length 0.60mm.

Carapace. Anterior margin now with small lateral projections similar to adult.

Antennule. Peduncular segment 1 outer surface with average of 14 obliquely placed plumose setae. Flagellum with few additional aesthetascs. Endopod 3-segmented.

Antenna. Peduncular segments unchanged. Flagellum with some additional segments.

Mandible. Molar part distinct and whole mandible similar in shape to adult.

Maxillule. Basis and coxa with many additional setae; ventral surfaces with row of setae developed similar to adult although fewer in number.

Maxilla. Scaphognathite with average of 25 plumose marginal setae. Endopod distally tapering into thin process, similar in shape to adult. Many additional setae on basis and coxa.

Maxilliped 1. Setal numbers increased and plumodenticulate setae present on lower surface of basis. Exopod segment 1 longer than in previous stage.

Maxilliped 2. Merus relatively longer than in previous stage (proportionally similar to adult). Setal numbers on propodus and dactyl increased and similar to adult.

Maxilliped 3 (Fig. 15g). Setal numbers increased on all endites. *Crista dentata* now well developed and with 11–12 obtuse spines, accessory tooth well developed.

Pereiopods 1 (Fig. 15e, f). Left cheliped (f), carpus proportionally longer than in previous stage and with 3 prominent spines on outer margin. Upper margin of propodal prolongation and lower margin of dactyl with fewer setae. Right cheliped (e), carpus with 3 robust spines on upper margin. Upper and lower margins of propodal palm cristate and dentate.

Pereiopod 3. Dactyl lower margin with one spiniform setae.

Pereiopod 4. Propodus with average of 13 and dactyl with 8 pseudochaetae.

Pleopods. Left pleopod 1 very reduced in two specimens available for study; 2–4 well developed and still uniramous.

Pleopods on right side of abdomen absent. Pleopod 5 (uropod), left noticeably larger than right. Exopod with average of 17 and of right 13 pseudochaetae arranged in two rows. Endopod with 5 pseudochaetae.

REMARKS

Larval morphology of the genus *Anapagurus* is poorly known when compared with other pagurid genera. Of the twenty species attributed to *Anapagurus* (see Gordan, 1956) the larval stages of only six are known and the complete larval development has been only briefly described for five of these species (see Sars, 1890; MacDonald *et al.* 1957; Pike & Williamson, 1960; Dechancé, 1961; Dechancé & Forest, 1962).

The first and fourth zoea and the megalopa of *A. chiroacanthus* was described by Sars (1890) from Norwegian plankton-collected material and brief accounts were given of the complete larval development by MacDonald *et al.* (1957) and Pike & Williamson (1959) and of the first stage zoea by Pike & Williamson (1960). These descriptions were based on laboratory hatched first zoeas and reared plankton-collected stages from Plymouth, Port Erin, the Irish Sea, Firth of Clyde and Naples.

The present reared material originating from the Millport region of the Firth of Clyde differs from previous larval accounts of *A. chiroacanthus* in the features listed below.

Sars (1890) gives the length of zoea I as '1½mm' (*cf.* 2.10mm average length of Millport material) and shows: *telson* posterior margin with longest pair of setae proportionally longer than in Millport material; *antennule* with 4 aesthetascs (*cf.* 3 in Millport material); *mandibles* incisor process much less prominent; *maxillule* exopod with 0, 1, 3 setae (*cf.* 1, 1, 2), coxa with 6 setae (*cf.* 7); *maxilla* endopod 3, 2 setae (*cf.* 3, 3), coxa 3, 7 setae (*cf.* 2, 7); *maxilliped* 1 basis with 1–2–2 setae (*cf.* 1–1–3–3 setae), endopod segments 1–4 each with an outer marginal distal seta and with 1, 2, 1, 2 inner marginal setae (*cf.* segments 1–4 with outer distal marginal microtrichia and 3, 2, 1, 2 setae on inner margin); *maxilliped* 2 basis with 1 distal inner marginal seta (*cf.* 2), endopod segment 3 with 1 outer marginal seta (*cf.* without a seta but with microtrichia).

Zoea IV, *antennule* with a transverse suture demarcating basis from endopod and exopod buds, 6 or 7 aesthetascs/setae and 1 plumose seta (*cf.* without a suture in Millport material, 2 plumose setae and 9 aesthetascs); *antenna* endopod bud incipiently segmented, peduncle ?without a small outermost spine (*cf.* without segmentation and with a small outermost peduncular spine); *maxillule* basis with 1–2 submarginal setae (*cf.* without submarginal setae), coxa with 6 setae (*cf.* 9); *maxilla* scaphognathite with 10 anterior and no posterior setae (*cf.* 14 anterior, one medial and 3 posterior setae) endopod with 3, 2 setae, basis 4, 4, coxa 4, 6 (*cf.* 3,3 4,5 3,7 setae on respective endites); *maxillipeds* exopods of 1, 2, 3 with 5, 6, 5 setae respectively (*cf.* 8, 8, 7 setae); *pereiopod* 5 developed (*cf.* indistinct); *pleopods* exopod of uropod with 6 setae (*cf.* 7 setae).

Megalopa, '2½mm' (*cf.* average 2.10mm); *rostrum* obtusely oval (*cf.* sub-acute in Millport specimens); *pereiopods* cheliped propodus noticeably broadened (*cf.* only moderately broadened), pereiopod 3 dactyl sub-equal to propodus (*cf.* much longer than propodus), pereiopod 4 dactyl only slightly longer than propodus (*cf.* much longer than propodus); *pleopods* developed on segment ?5 (*cf.* not present on segment 5); *telson* longer than broad and with 12 marginal plumose setae (*cf.* about as long as broad and with 8 setae).

MacDonald *et al.* (1957) and Pike & Williamson (1959) show; zoea I, *telson* posterior margin with longest pair of setae (ie 2nd plumodenticulate pair) longer than in Millport material.

Zoea II, *telson* 4th seta on posterior margin (ie 3rd plumodenticulate) slightly shorter than 5th (ie. 4th plumodenticulate) (*cf.* slightly longer in Millport specimens).

Zoea III, *uropods* extending into posterior 4th of telson (*cf.* posterior 7th); *telson* 3rd seta (ie 2nd plumodenticulate developed as spine) on posterior margin relatively much longer than in Millport material, setae on telson dorsal surface ?absent (*cf.* one pair present).

Zoea IV, *pleopods* present on segments 2–4, 6 (*cf.* on 2, 3, 6 in Millport material); uropod with 6 exopod setae (*cf.* 7); *telson* 3rd seta (ie 2nd plumodenticulate seta developed as spine) on posterior margin much broader than in Millport material, dorsal surface of telson ?without setae (*cf.* 2 pairs).

Megalopa, *rostrum* figured as obtuse and described as 'very blunt' (*cf.* subacute in Millport specimens); (*cf.* 12); *pereiopods* cheliped propodus noticeably broadened (less broad in Millport specimens); *pleopods* uropod with 10–12 exopod setae (*cf.* average 15); *telson* longer than broad and ?without dorsal setae (*cf.* almost as broad as long and with 2 pairs of setae).

The present laboratory reared material of *Anapagurus chiroacanthus* enables comparisons to be made between the megalopa, early juvenile and adult stages. The following morphological features are shared by the megalopal and first stage crab. *Antennule*; peduncular segment 1 with oblique ridge of setae on outer surface and disto-dorsal setae on peduncular segment 3, endopod 2-segmented. *Antenna*: the same number of flagellum segments and setation. *Maxilla*: distal seta on endopod and posteriorly narrowed scaphognathite. *Pereiopod* 2: subapical spine on meral lower margin, propodal distal spine on lower margin and similar overall setation of segments. *Pereiopod* 3: spine on carpal upper distal margin and propodal distal spine on lower margin. *Pereiopod* 5: similar overall setation of propodus and dactyl. *Telson*: 2 pairs of setae on dorsal surface.

The following features of *A. chiroacanthus* are common to the first stage crab and the adult. *Antennule*: peduncular segment 1 with oblique ridge of setae* on outer surface and subdistal spine and distal obtuse process on lower margin. *Antenna*: peduncular segment 2 with outer dorso-lateral process and developed supernumary segment. *Mandible*: with small but prominent seta on protopod. *Maxillule*: with propodal lobe and distal seta on endopod. *Maxilla*: with prominent sub-distal row of plumose coxal setae. *Maxilliped* 2: segment 2 of exopod with single outer marginal seta, basis with only 6 setae. *Maxilliped* 3: segment 2 of exopod with outer mid-point seta, accessory tooth developed on ischium of endopod. *Pereiopod* 2: lower margin of merus with subapical spine* and propodal distal spine.* *Pereiopod* 3: spine on upper distal carpal* margin and on lower distal propodal* margin.

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* Also present in megalopal stage.

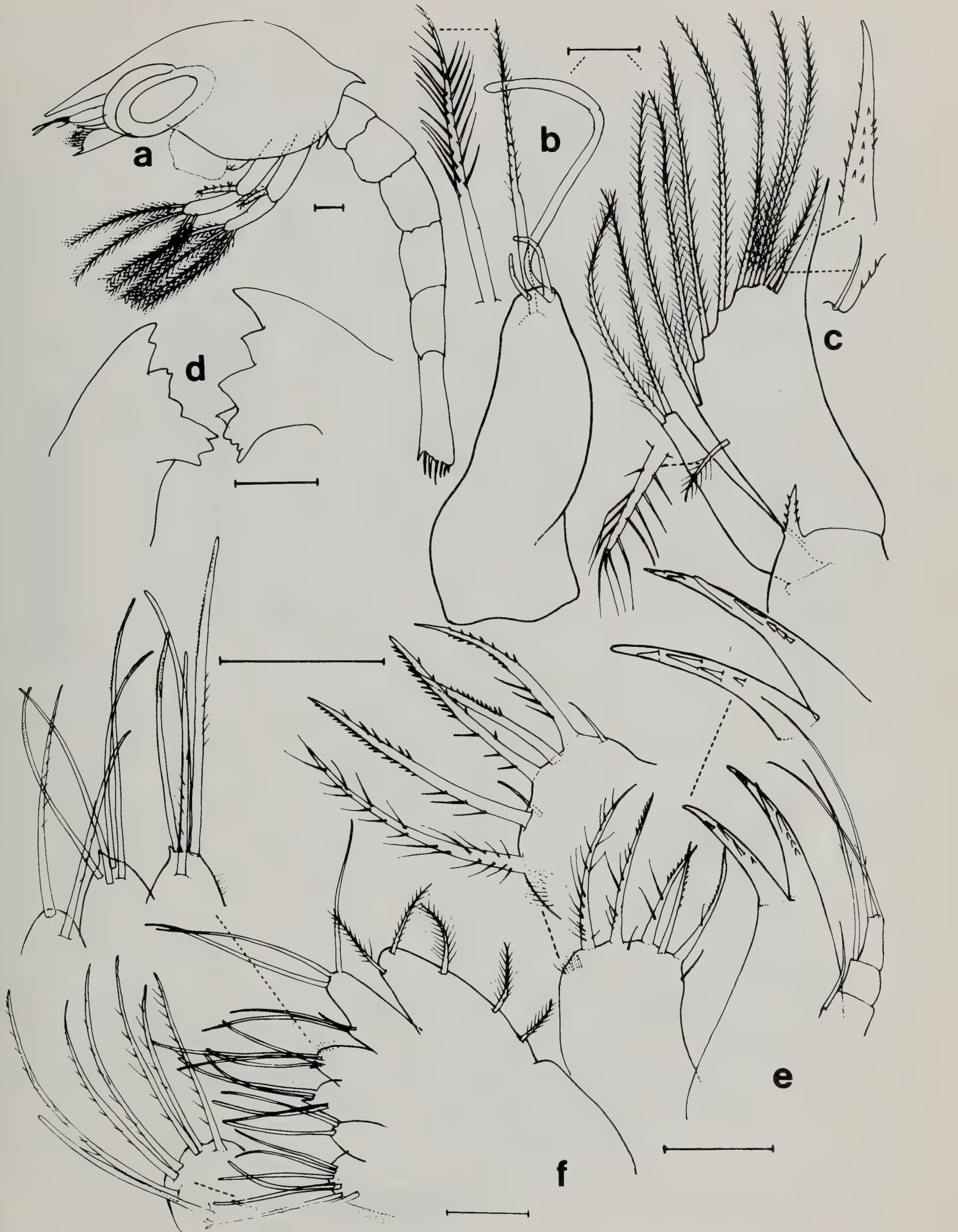

Fig. 1 *Anapagurus chiroacathus* ZOEA I: **a** whole larva from left lateral aspect; **b** left antennule; **c** left antenna (upper inset shows details of spine & lower inset the simple seta on this margin); **d** mandibles from ventral aspect; **e** left maxillule; **f** left maxilla. (Scales **a** = 100μm, others 50μm).

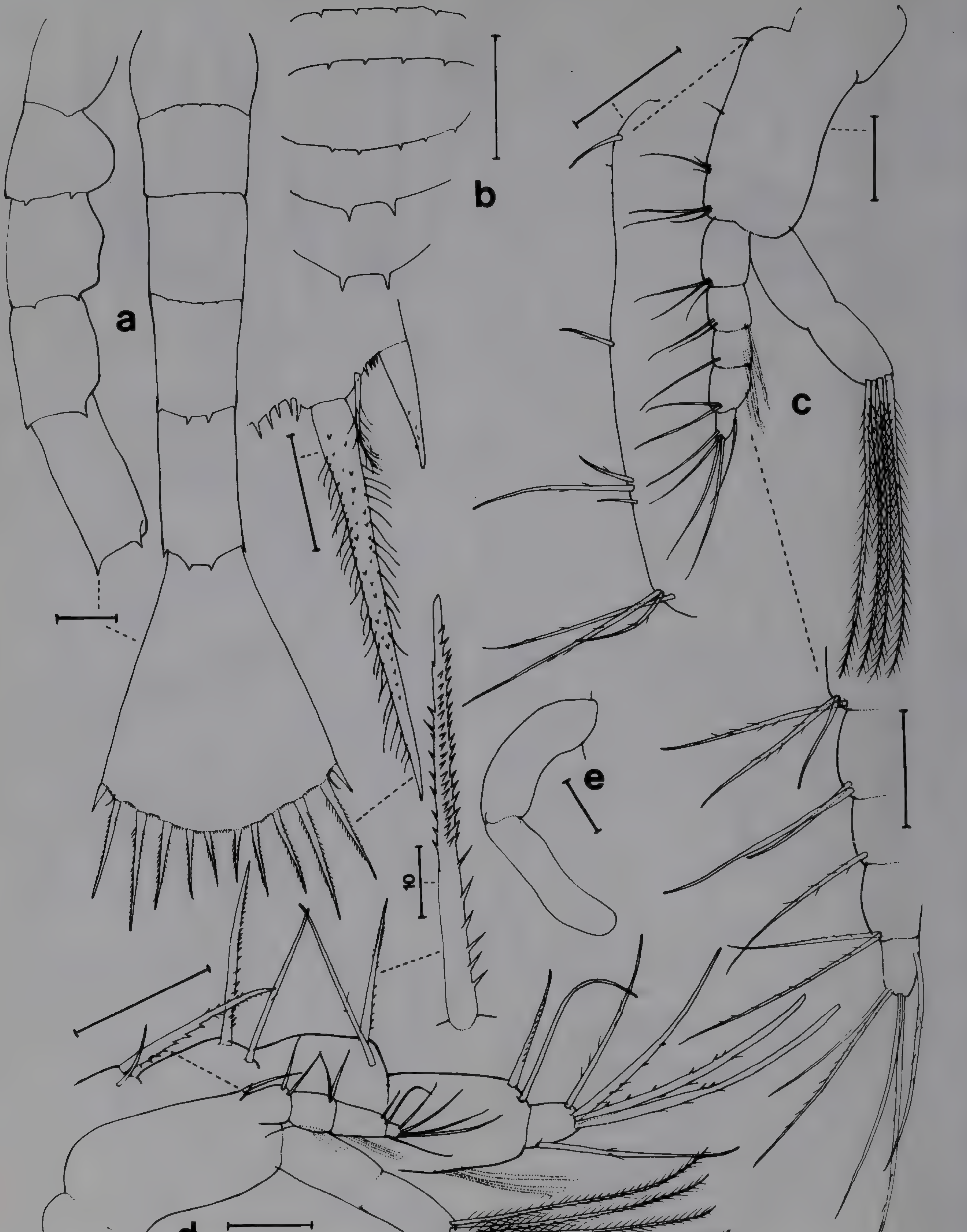

Fig. 2 *Anapagurus chiroacanthus* ZOEA I: **a** abdomen and telson, dorsal (right) and lateral (left) aspects; **b** posterio-dorsal margins of abdominal segments 1–5; **c–e** maxillipeds 1–3 from left side. (Scales **a–c** = 100μm, **e** & inset = 50μm, except where indicated).

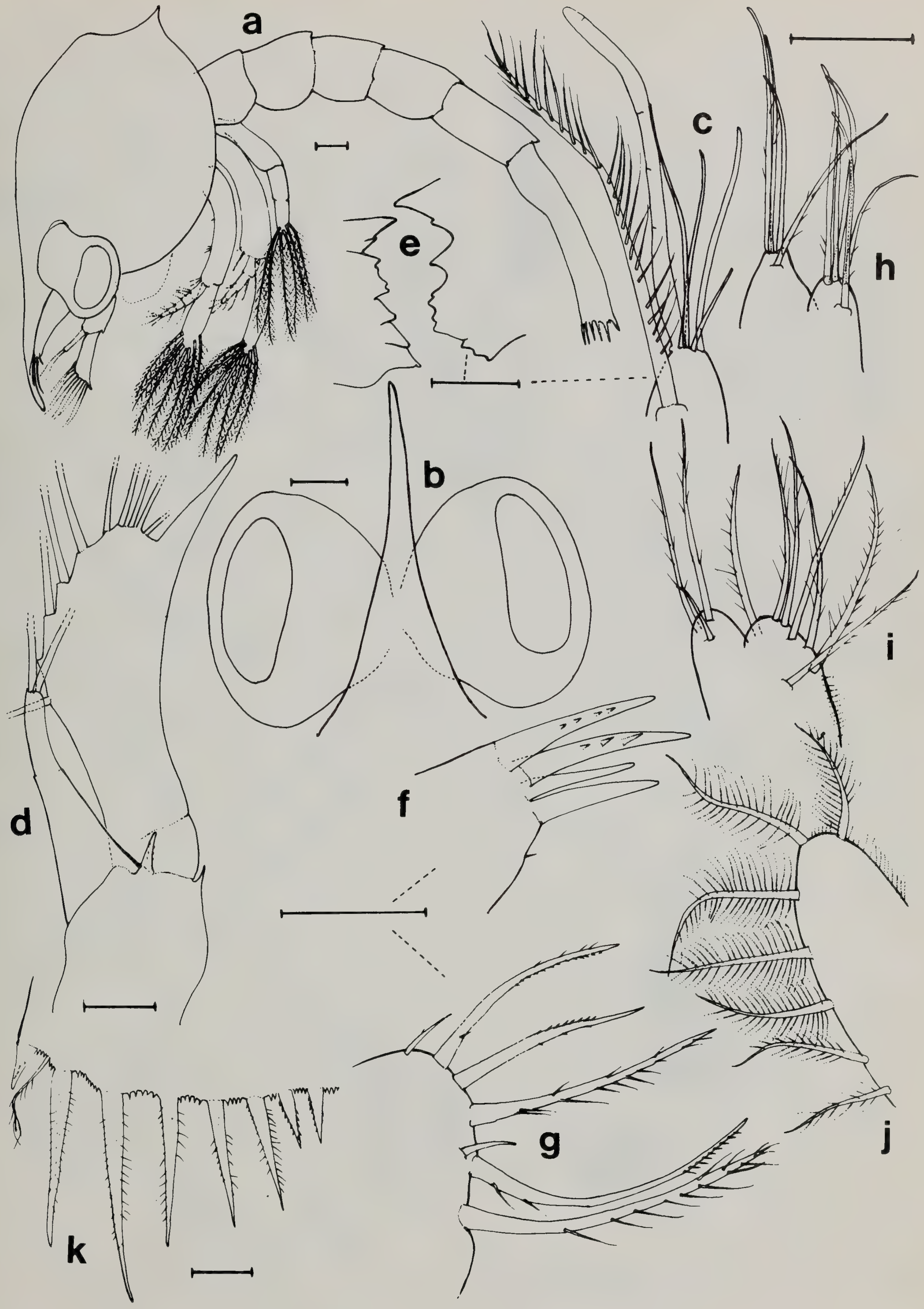

Fig. 3 *Anapagurus chiroacanthus* ZOEA II: **a** whole larva from left lateral aspect; **b** dorsal view of eyes and rostrum; **c** distal part of left antennule; **d** left antenna; **e** incisor and molar parts of mandibles; **f, g** distal parts of basis and coxa of right maxillule; **h, i, j** basis, coxa and scaphognathite of right maxilla; **k** left posterior margin of telson. (Scales **a**, **b** = 100μm, others = 50μm).

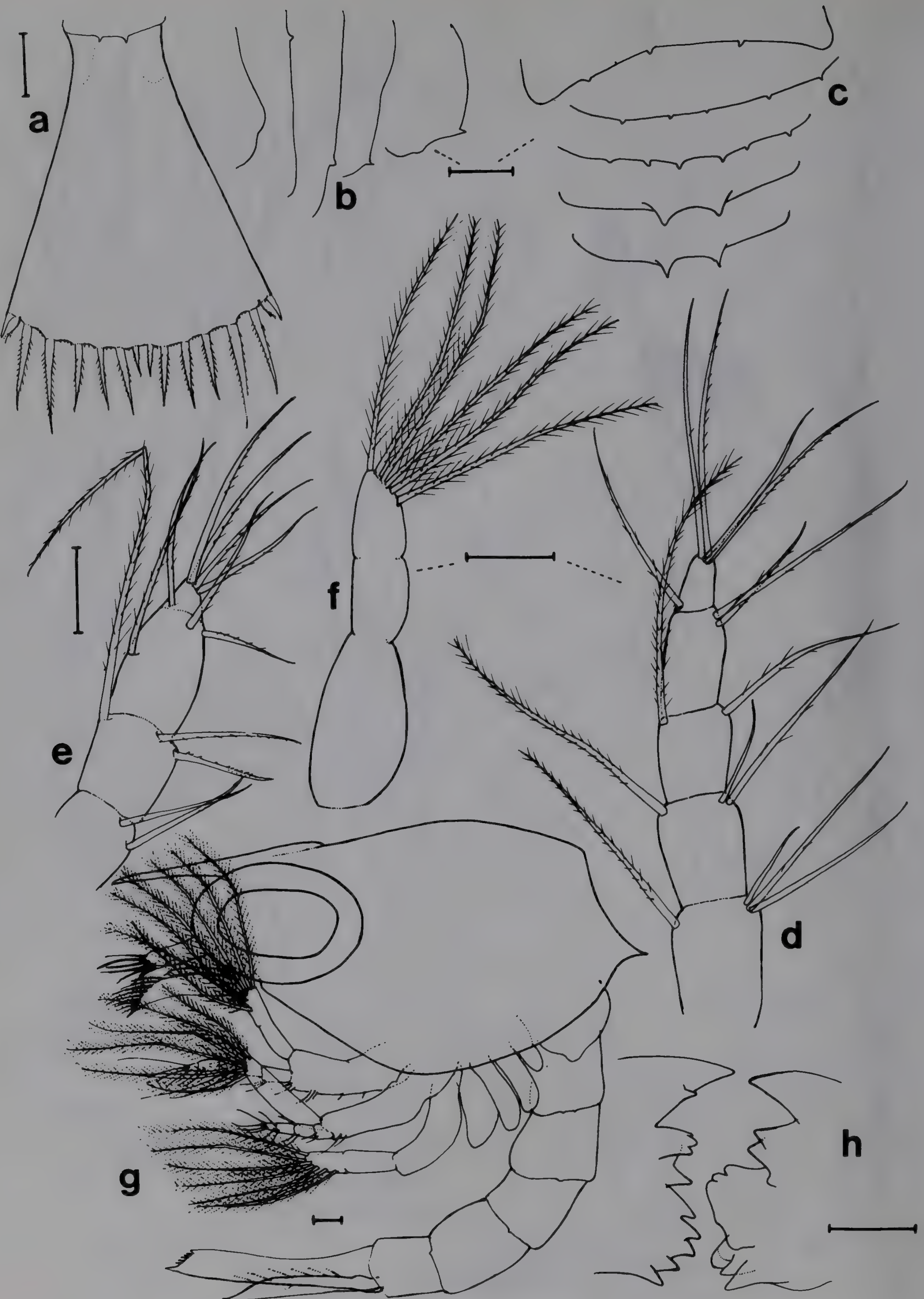

Fig. 4 *Anapagurus chiroacanthus* ZOEA II: **a** telson in dorsal aspect; **b** posterio-lateral and **c** posterio-dorsal margins of abdominal segments 1–5; **d** endopod of right maxilliped 1 and **e** of maxilliped 2; **f** right maxilliped 3. ZOEA III **g** whole larva from left lateral aspect; **h** mandibles from ventral aspect. (Scales **a**, **g** = 100μm, others = 50μm).

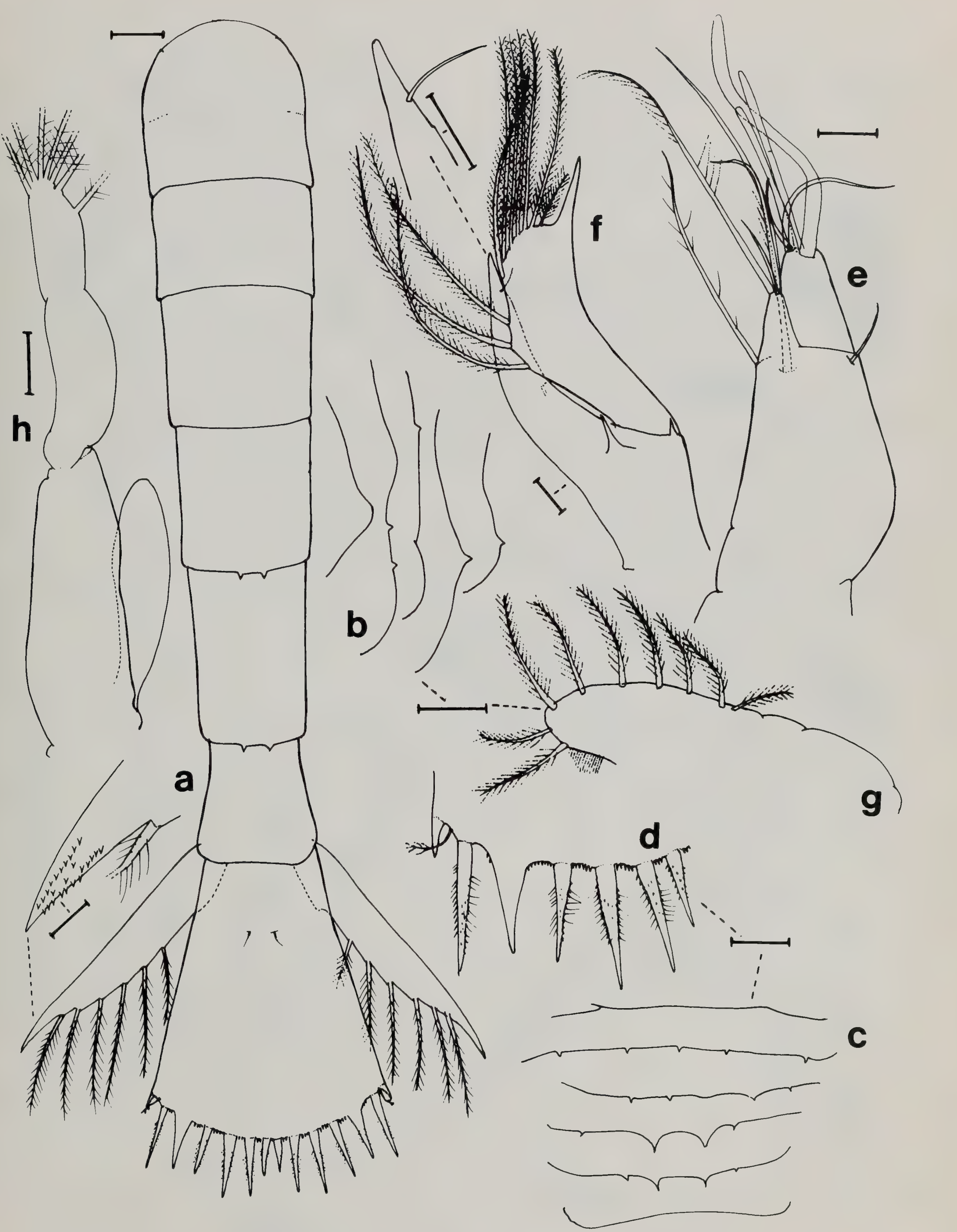

Fig. 5 *Anapagurus chiroacanthus* ZOEA I: **a** abdomen, telson and uropods from dorsal aspect; **b** posterio-lateral margin of abdominal segments 1–5; **c** posterio-dorsal margins of abdominal segments 1–6; **d** left half of telson posterior margin; **e** right antennule; **f** right antenna; **g** scaphognathite of left maxilla; **h** left maxilliped 3. (Scales = 100μm, others = 50μm, except inset to **a** = 20μm).

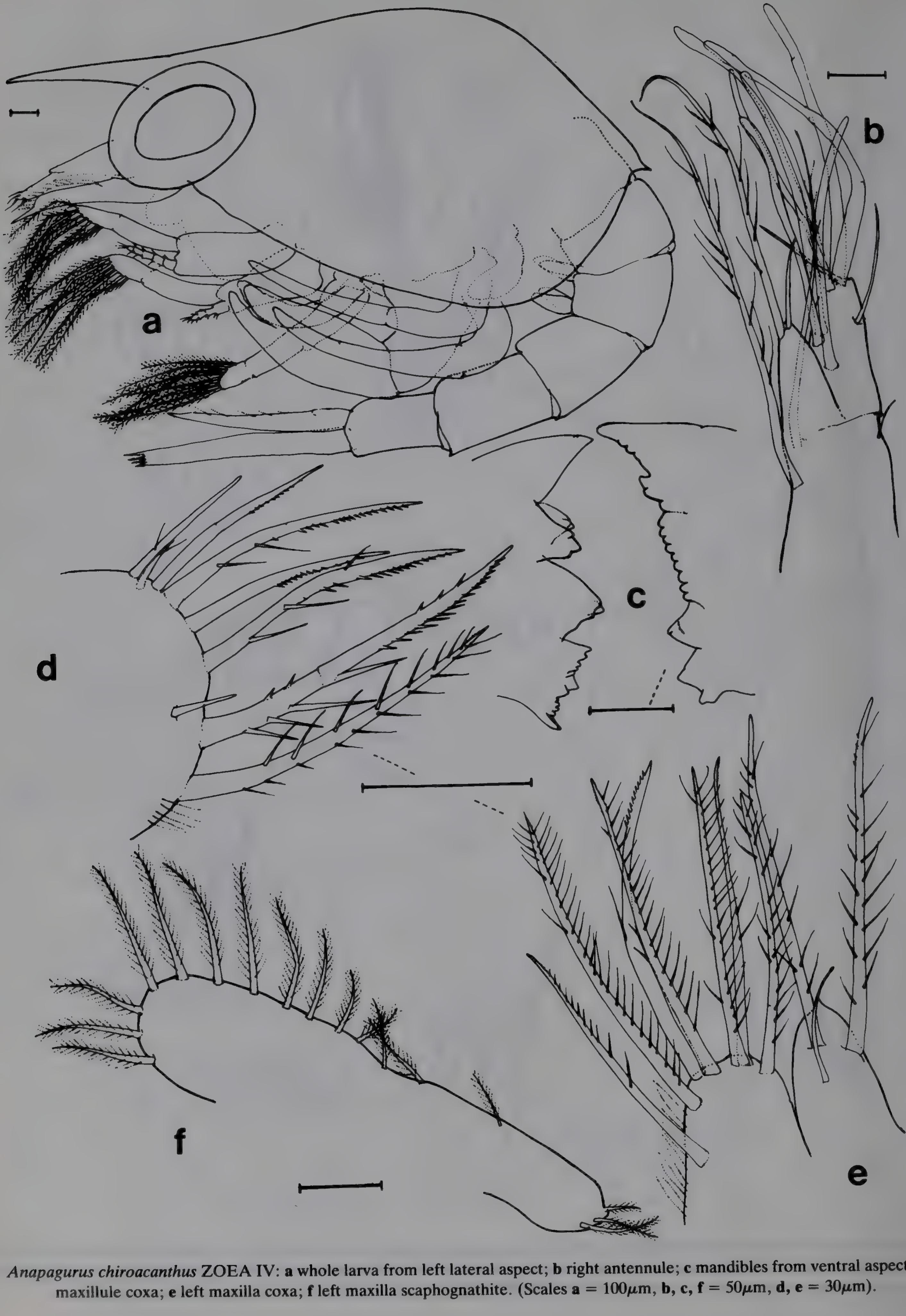

Fig. 6 *Anapagurus chiroacanthus* ZOEA IV: **a** whole larva from left lateral aspect; **b** right antennule; **c** mandibles from ventral aspect; **d** right maxillule coxa; **e** left maxilla coxa; **f** left maxilla scaphognathite. (Scales **a** = 100μm, **b, c, f** = 50μm, **d, e** = 30μm).

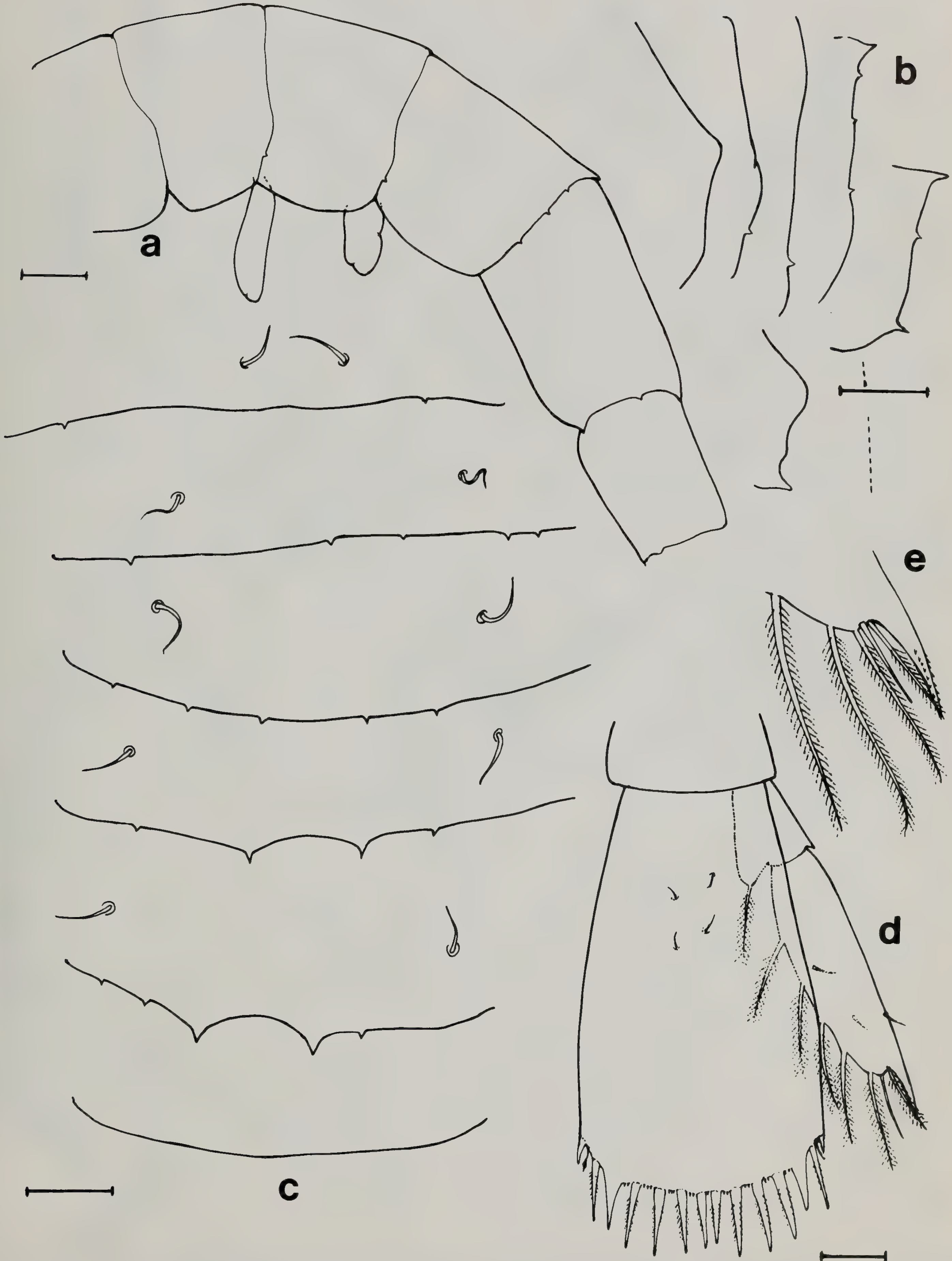

Fig. 7 *Anapagurus chiroacanthus* ZOEA IV: **a** abdominal segments 1–6 from left lateral aspect; **b** posterio-lateral margins and **c** posterio-dorsal margins of abdominal segments 1–6; **d** telson and right uropod from dorsal aspect; **e** distal part of uropod. (Scales 50μm, except **c** = 30μm).

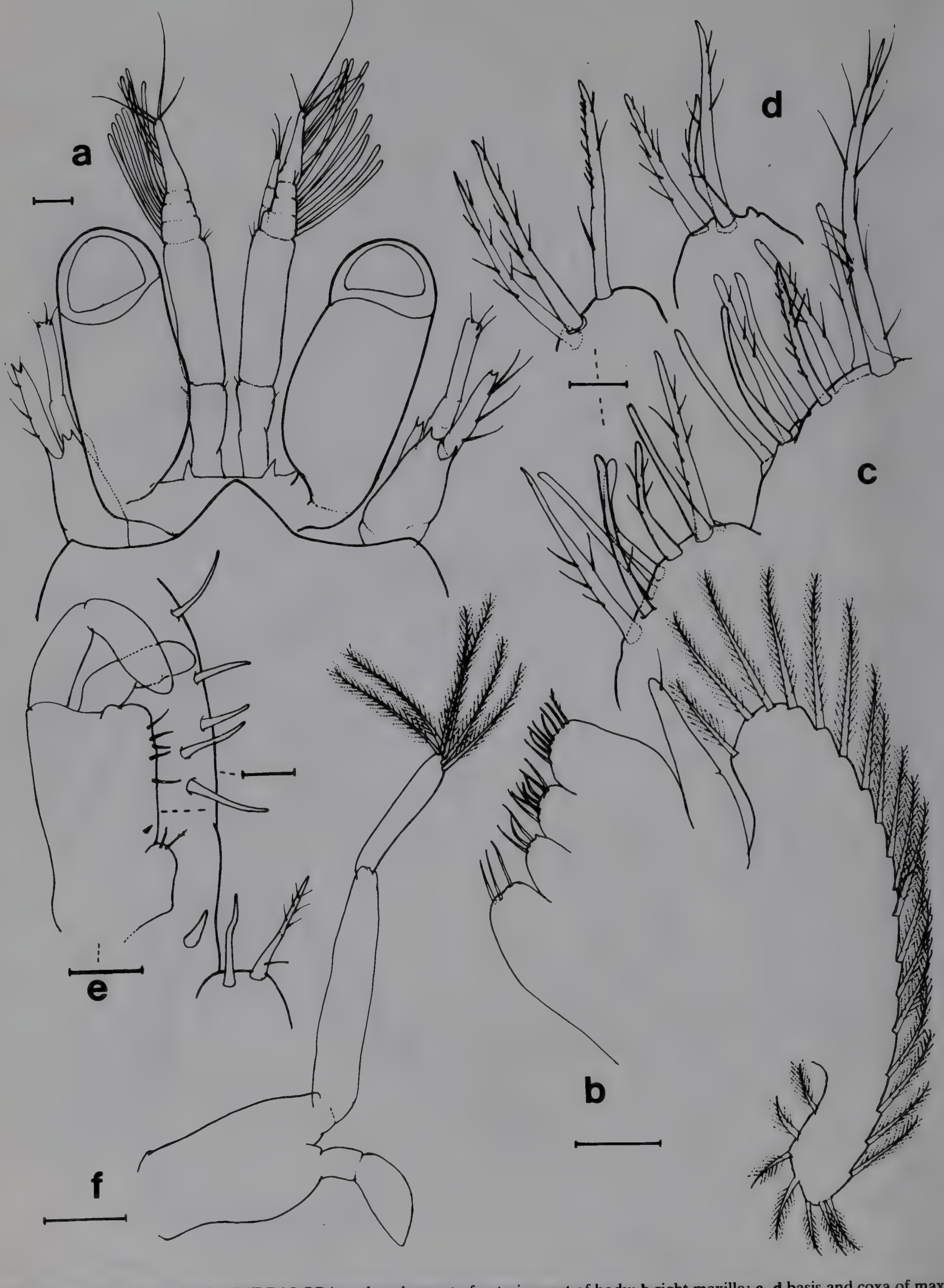

Fig. 8 *Anapagurus chiroacanthus* MEGALOPA: **a** dorsal aspect of anterior part of body; **b** right maxilla; **c, d** basis and coxa of maxilla; **e, f** right maxilliped 1 & 2. (Scales **a–c, f** = 50μm, **e** = 100μm, inset = 20μm).

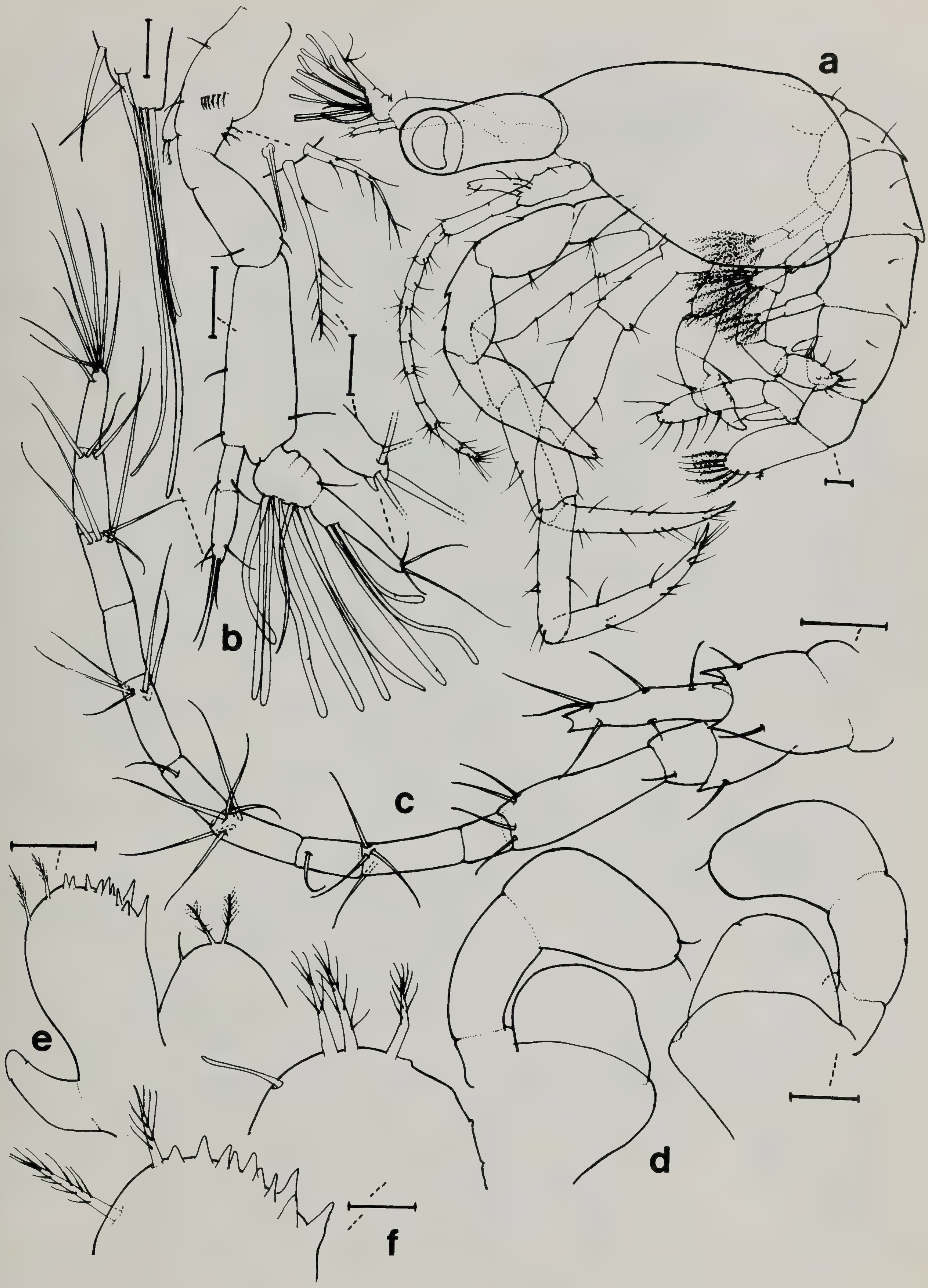

Fig. 9 *Anapagurus chiroacanthus* MEGALOPA: **a** whole larva from left lateral aspect; **b** left antennule; **c** left antenna; **d** mandibles from ventral aspect; **e** right maxillule; **f** basis & coxa of maxillule from another specimen. (Scales **a–c** = 100μm, **d**, **e** = 50μm, **f** & insets to **b** = 20μm).

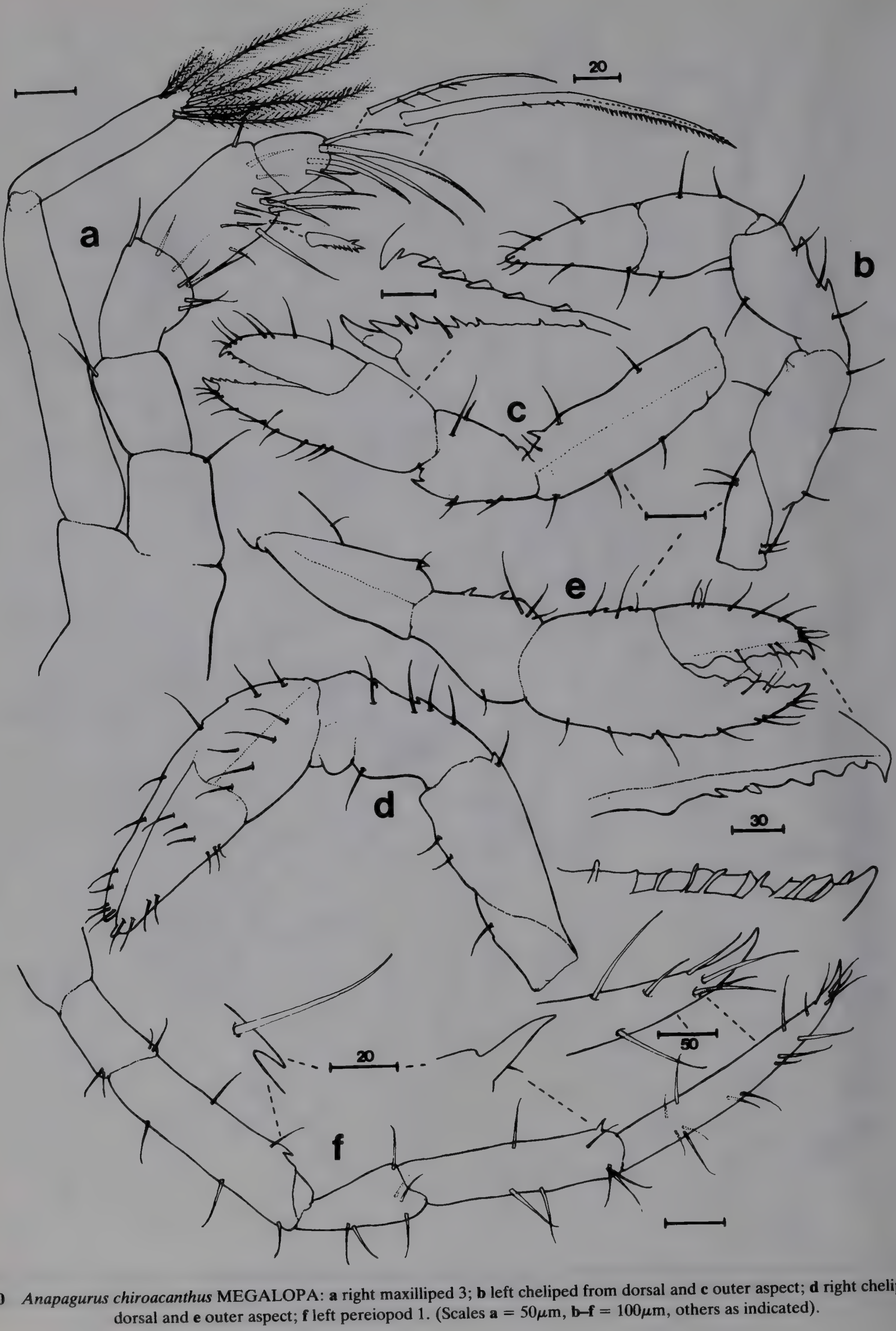

Fig. 10 *Anapagurus chiroacanthus* MEGALOPA: **a** right maxilliped 3; **b** left cheliped from dorsal and **c** outer aspect; **d** right cheliped from dorsal and **e** outer aspect; **f** left pereiopod 1. (Scales **a** = 50μm, **b–f** = 100μm, others as indicated).

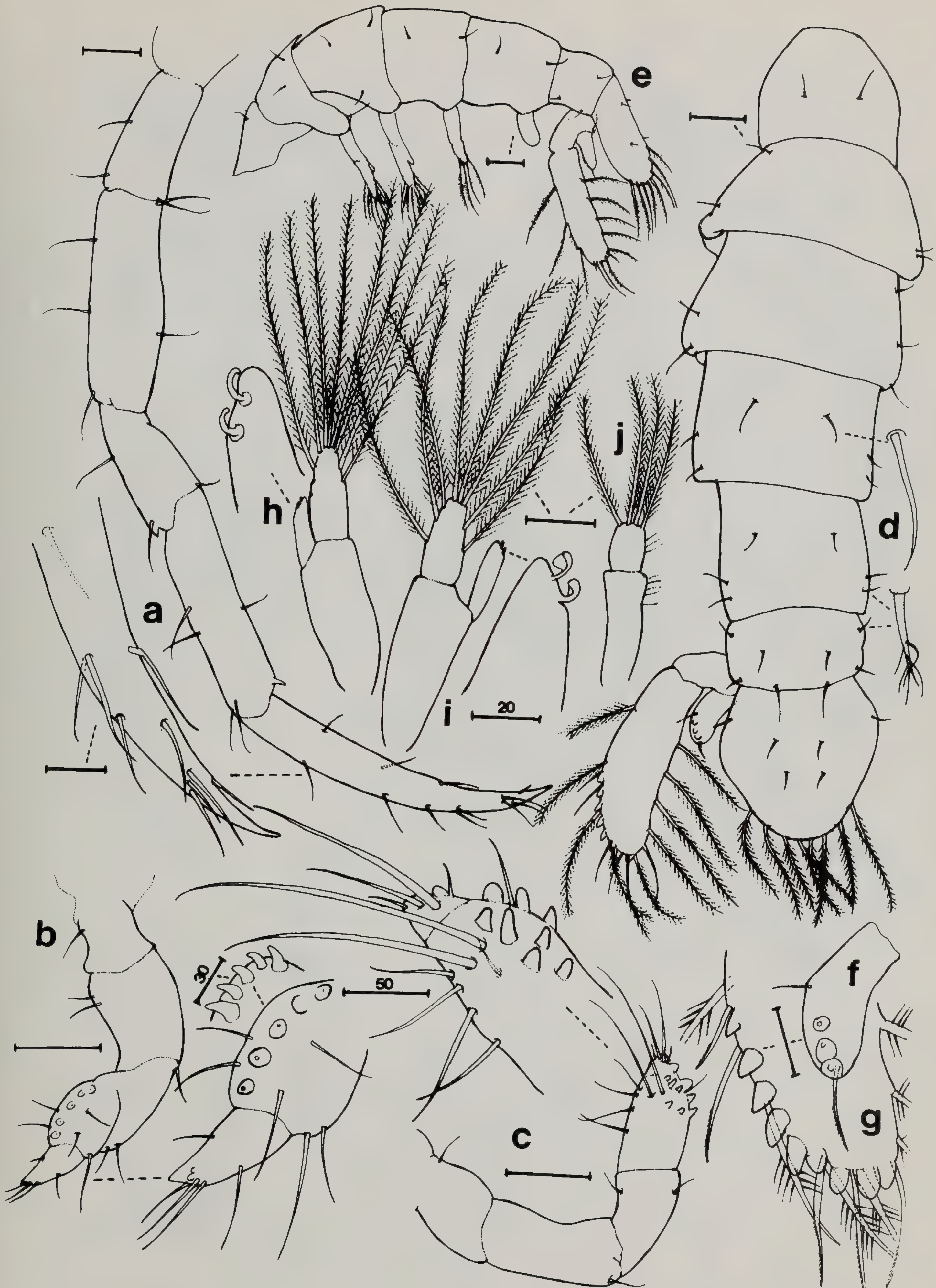

Fig. 11 *Anapagurus chiroacanthus* MEGALOPA: **a–c** left pereiopod 3–5; **d** abdomen telson & left uropod from dorsal and **e** from left lateral aspect; **f** endopod of left uropod and **g** distal part of exopod; *h–j* pleopods 1–3. (Scales **a, d, e, h–j** = 100μm, **b, c, f, g** = 50μm, others as indicated).

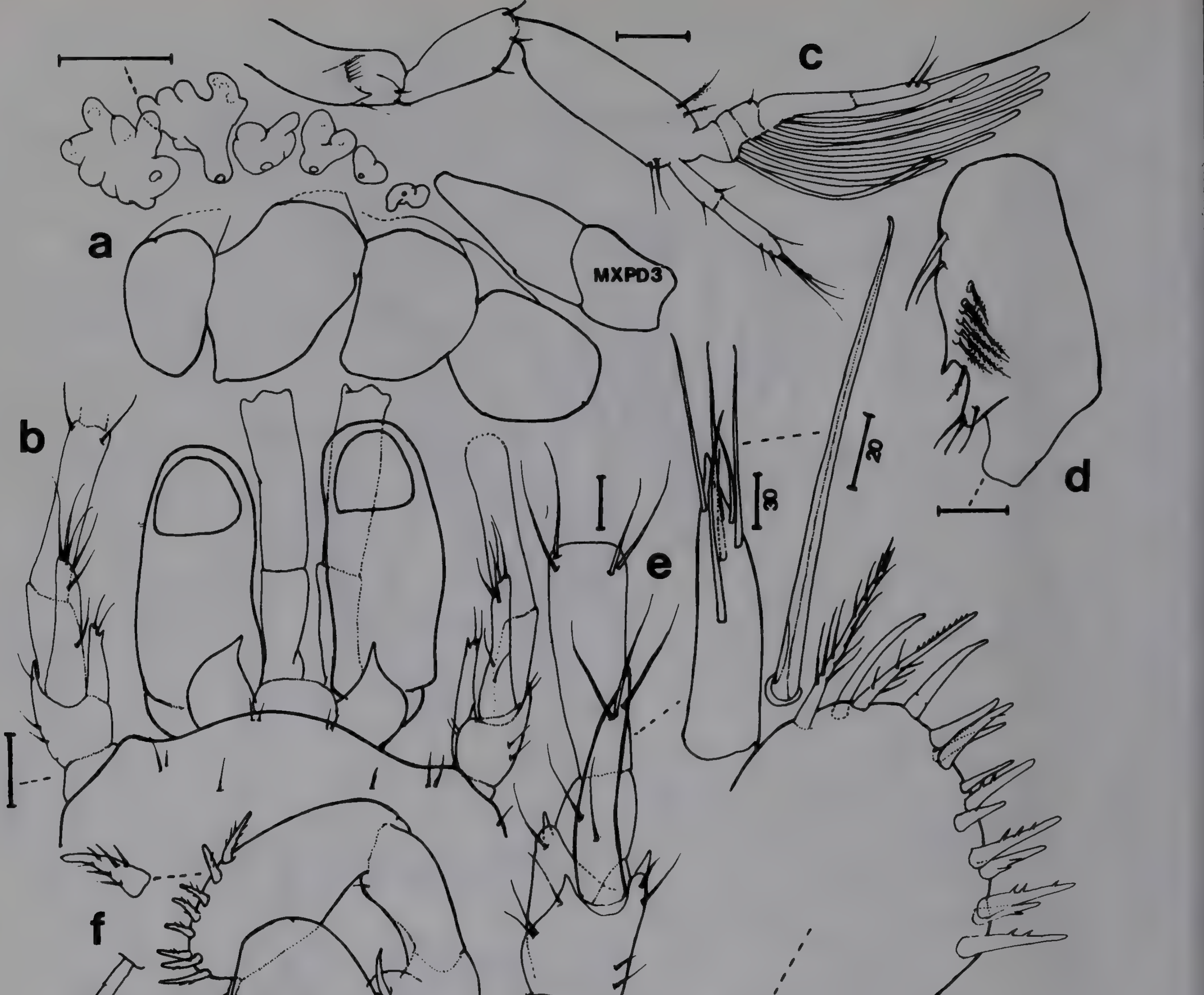

Fig. 12 *Anapagurus chiroacanthus* MEGALOPA: **a** gills, coxal segments of maxilliped 3 and pereiopods, CRAB 1: **b** anterior part of body; **c** right antennule; **d** antennular peduncle segment 1 from dorsal aspect; **e** right antennal peduncle from dorsal aspect and inset of acicle from ventral aspect; **f** mandibles from ventral aspect; **g** left maxillule. (Scales **a–c** = 100μm, **d–f** = 50μm, **g** = 30μm, others as indicated).

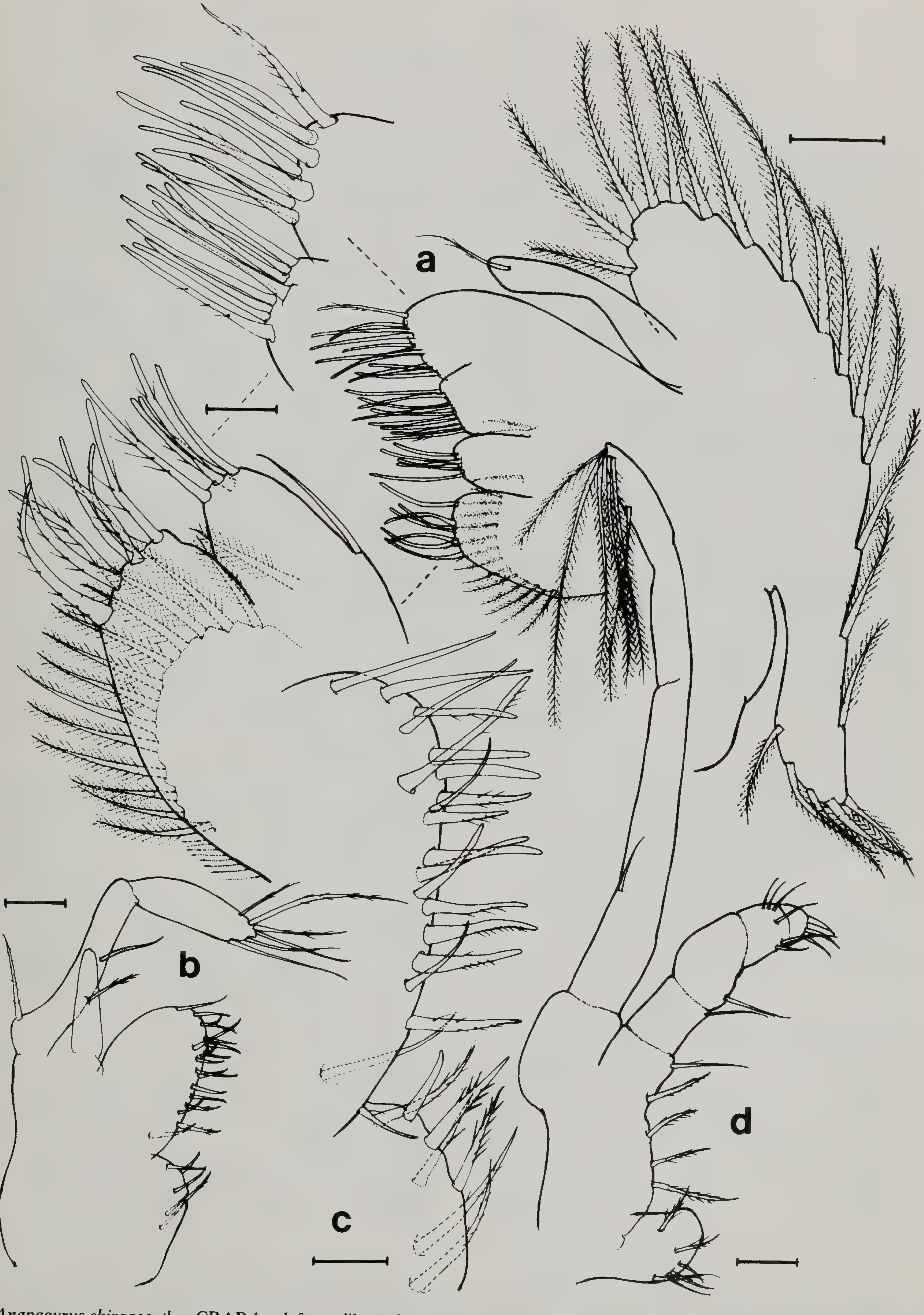

Fig. 13 *Anapagurus chiroacanthus* CRAB 1: **a** left maxilla; **b** right maxilliped 1; **c** basis & coxa of right maxilliped 1 from another specimen; **d** right maxilliped 2. (Scales **a**, **b**, **d** = 50μm, **c** & inset to **a** = 20μm).

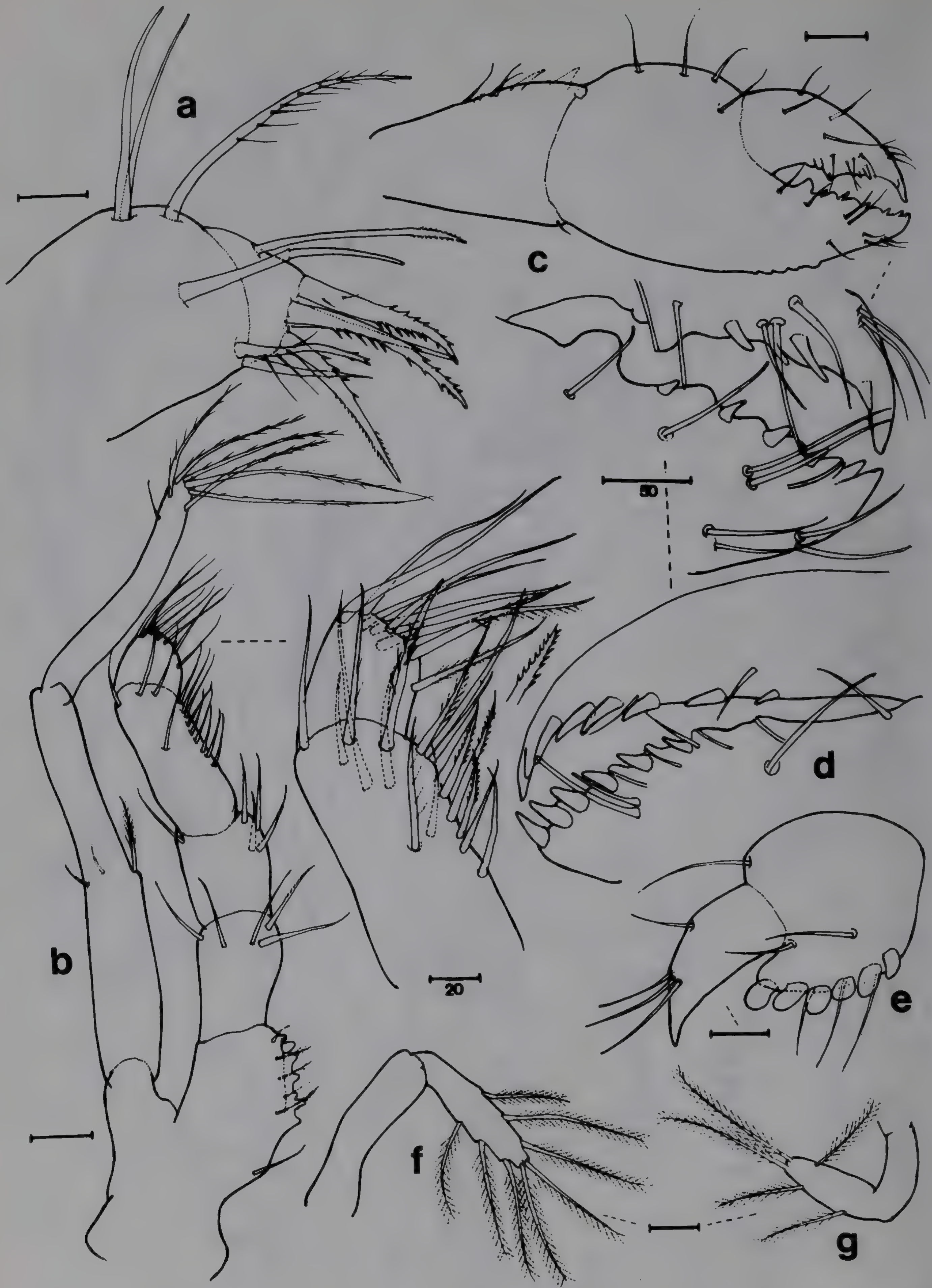

Fig. 14 *Anapagurus chiroacanthus* CRAB 1: **a** right maxilliped 2, dactyl & propodal endopod segments; **b** left maxilliped 3 (inset shows dactyl and propodus); **c** right pereiopod 1 (cheliped)-inset shows details of apposing dactyl and propodal distal margins; **d** distal apposing margins of left cheliped dactyl & propodus; **e** left pereiopod 4 dactyl and propodus; **f** left pleopod 1; **g** left pleopod 4. (Scales **a** = 30μm, **b, f, g** = 50μm, **c** = 100μm, **e** = 30μm, others as indicated).

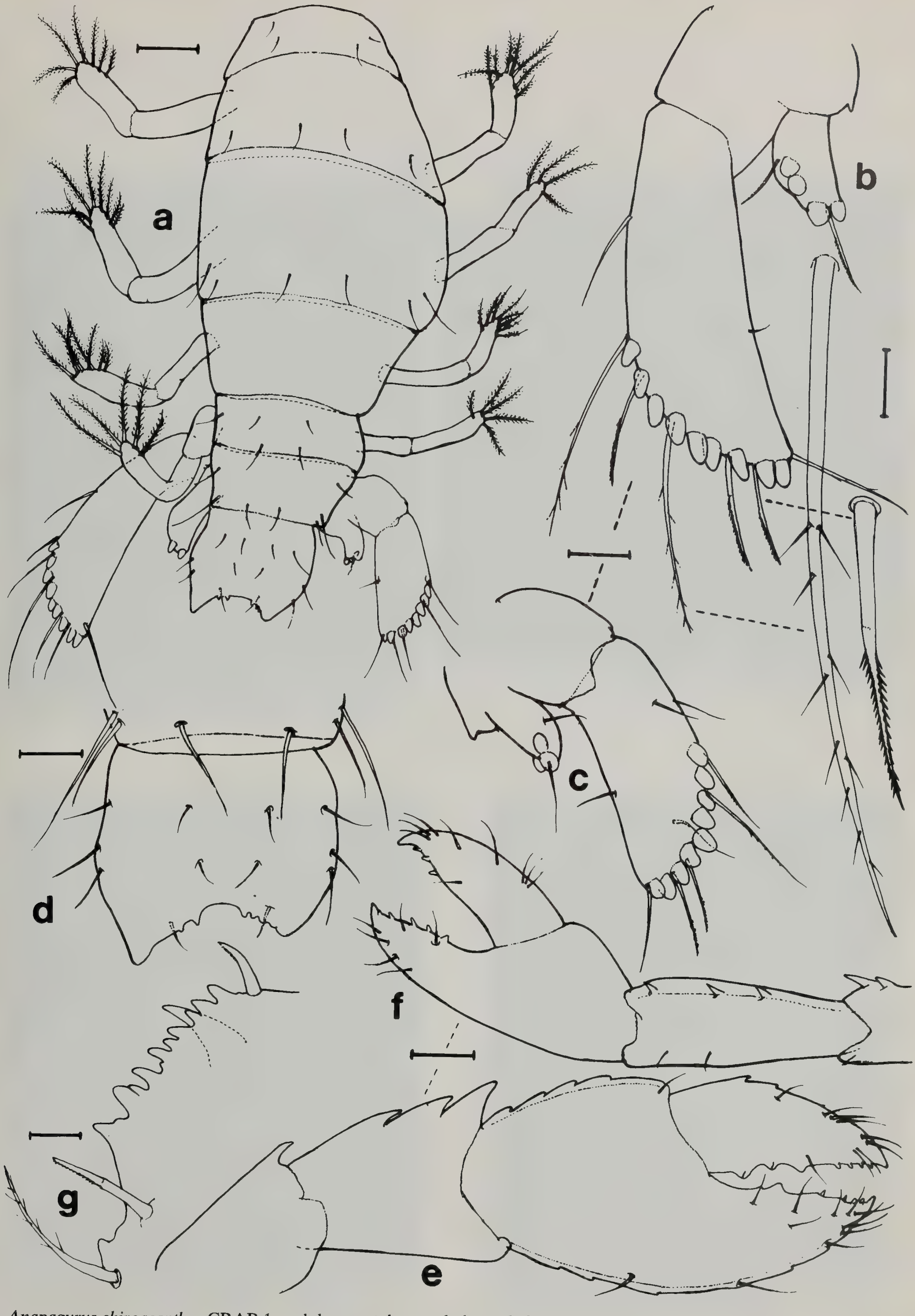

Fig. 15 *Anapagurus chiroacanthus* CRAB 1: **a** abdomen, telson and pleopods from dorsal aspect; **b** left uropod; **c** right uropod; **d** telson. CRAB 2: **e** right cheliped; **f** left cheliped; **g** ischium of maxilliped 3 from ventral aspect showing accessory tooth and *crista dentata*. (Scales, **a**, **e**, **f** = 100μm; **b**–**d** = 50μm, **g** & insets to **b** = 20μm).

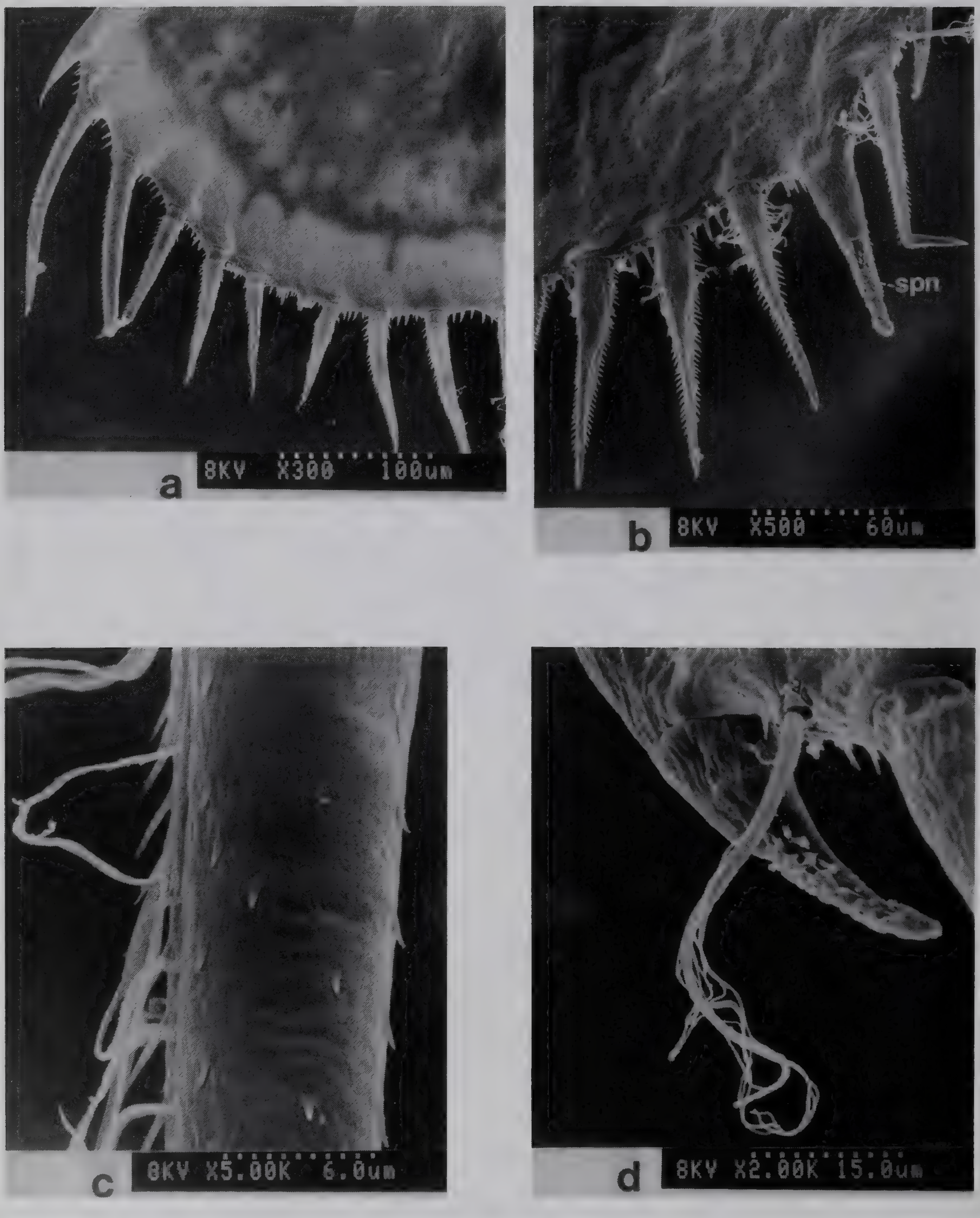
8KV X300 100um
a
spn
8KV X500 60um
b
8KV X5.00K 6.0um
c
8KV X2.00K 15.0um
d

Fig. 16 *Anapagurus chiroacanthus* posterior margin of telson showing arrangement of setae in: **a** ZOEA I; **b** ZOEA III showing spine (*spn*) replacing 2nd plumodenticulate seta; **c** ZOEA I surface of one (5th) plumodenticulate seta; **d** details of pappose seta.

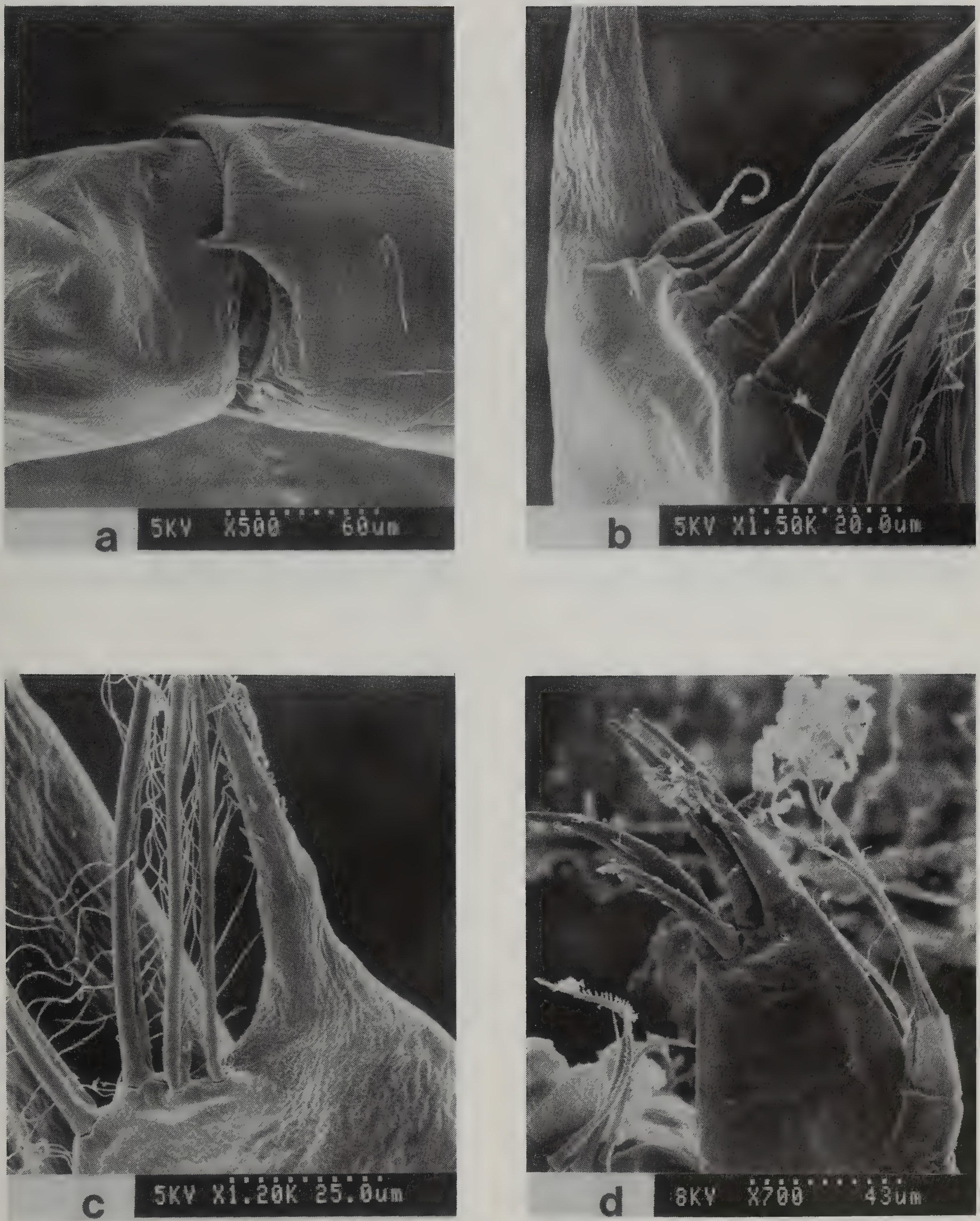
a
5KV X500 60um
b
5KV X1.50K 20.0um
c
5KV X1.20K 25.0um
d
8KV X700 43um

Fig. 17 *Anapagurus chiroacanthus* ZOEA I: **a** posterio-lateral spine on abdominal segment 5; **b** distal simple setae adjacent to antennal exopod spine; **c** same region of ZOEA II showing replacement of simple seta with plumose type; **d** ZOEA IV maxillule exopod and basis showing stout cuspidate setae.

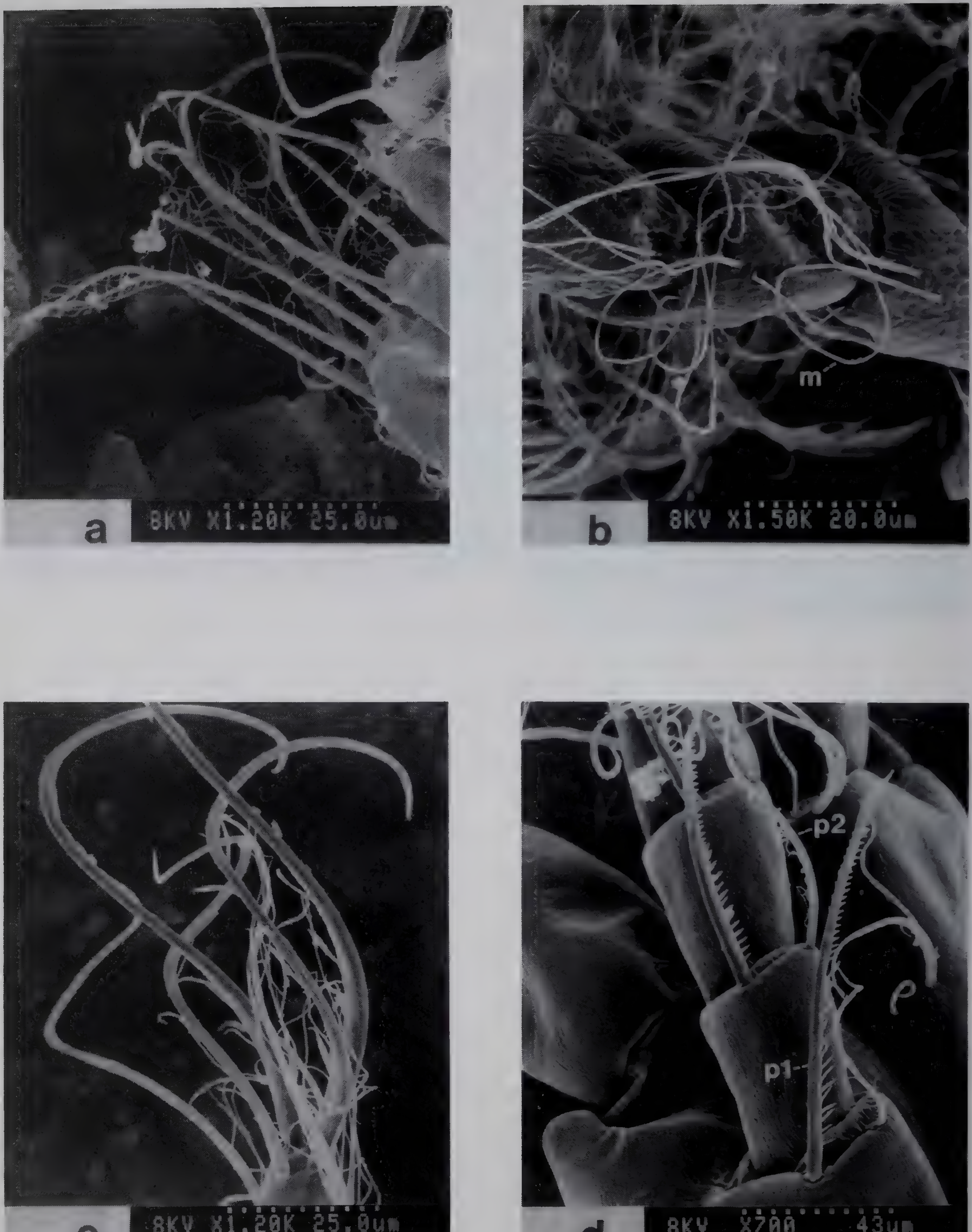
8KV X1.20K 25.0um
a
8KV X1.50K 20.0um
b
m
8KV X1.20K 25.0um
c
p2
p1
8KV X700 43um
d

Fig. 18 *Anapagurus chiroacanthus* ZOEA I: **a** maxilla coxa showing plumodenticulate seta with long setules; **b** maxilliped endopod segments 2, 3 showing microtrichia (*m*) on outer surface. ZOEA IV **c** maxilliped 1 endopod segment 5 showing plumodenticulate setae variably invested with setules; **d** maxilliped 2, distal basis and endopod segments 1–3 showing two distinct types of plumodenticulate setae (p1, p2).

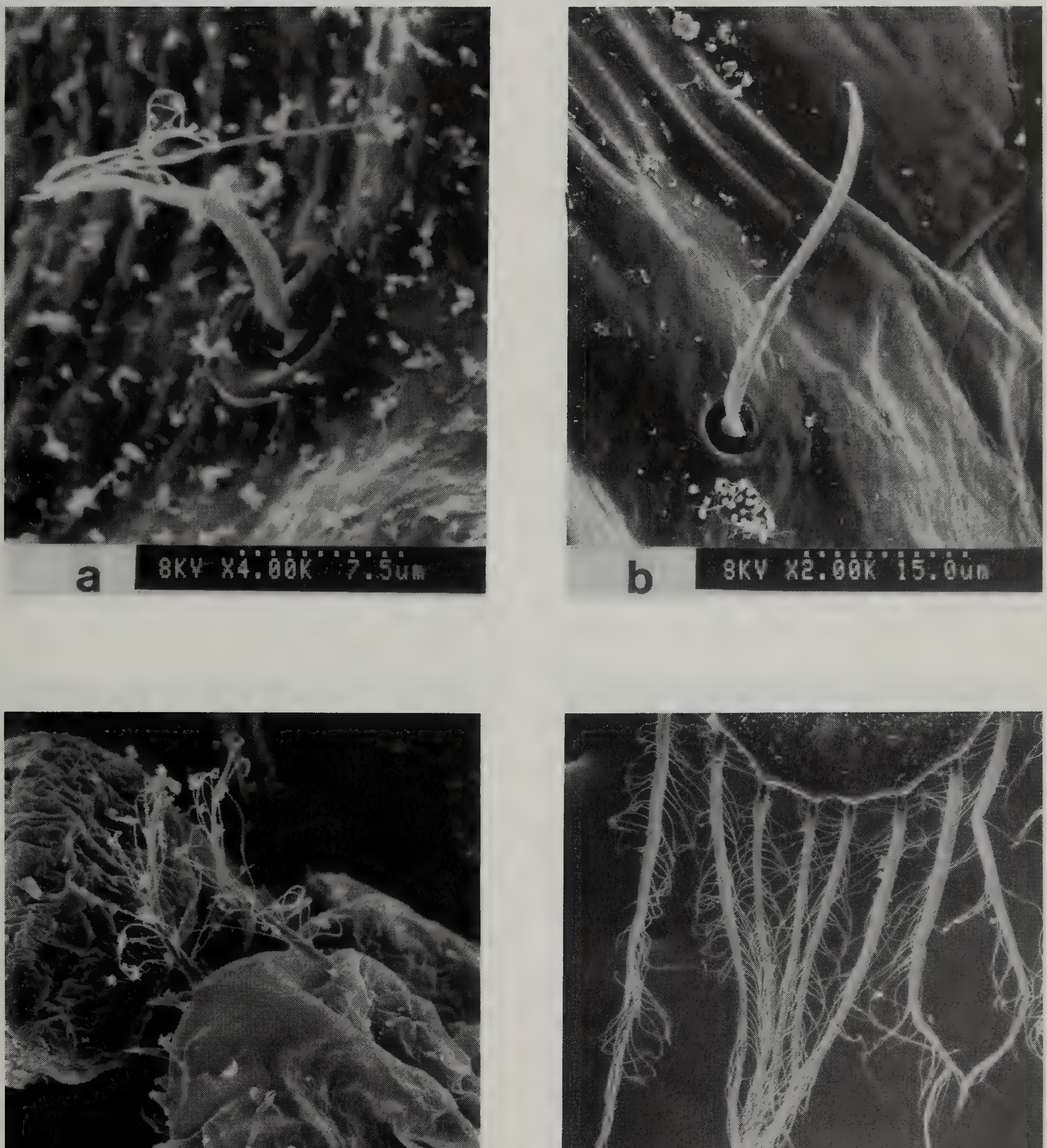
a
8KV X4.00K 7.5um
b
8KV X2.00K 15.0um
c
8KV X1.20K 25.0um
d
8KV X400 75um

Fig. 19 *Anapagurus chiroacanthus* MEGALOPA: **a** abdominal segment 3 pappose seta; **b** abdominal segment 4 simple seta; **c** maxillule basis showing small spiniform setae; **d** plumose setae on telson posterior margin.

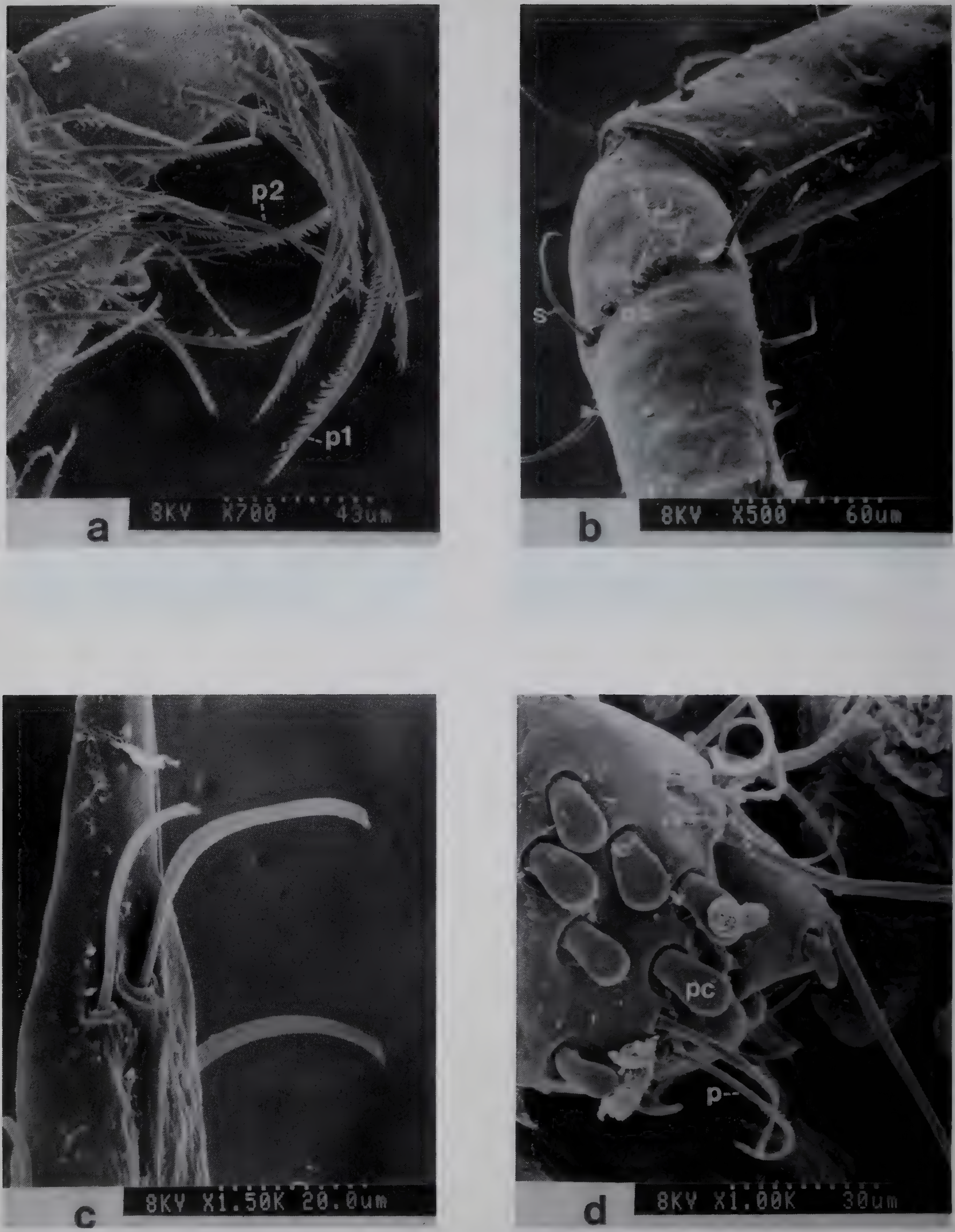
p2
p1
a
8KV X700 43um
s
pa
b
8KV X500 60um
c
8KV X1.50K 20.0um
pc
p
d
8KV X1.00K 30um

Fig. 20 *Anapagurus chiroacanthus* MEGALOPA: **a** maxilliped 3 distal inner propodus and dactyl showing two types of plumodenticulate setae (p1, p2); **b** pereiopod 2 proximal propodal dorsal surface showing simple (*s*) and pappose (*pa*) setae; **c** pereiopod 2 subdistal lower dactyl surface showing simple setae; **d** pereiopod 5 distal propodal surface and dactyl showing pseudochaetae (*pc*) and plumodenticulate (*p*) setae.

DISCUSSION

Ontogenetic variability of *A. chiroacanthus* larvae has not been studied previously and the apparent discrepancies between the account by Sars (1880) and the present material from Millport cannot be explained satisfactorily. Some of these differences may be due to omissions in drawing correct numbers of setae. The comparison suggests, however, that Sars' figures may represent more than two zoeal stages. For example, his figures of the first stage maxillipeds 1 and 2 show the endopod segments 1–4 each with a disto-external seta. In this stage of the present material only microtrichia are present on this region of some of these segments, but are replaced by setae at the second stage. He also shows the maxilla coxa with 3, 7 setae, a feature noted also for second stage specimens of the present material. Similarly, only 6 exopod setae are shown on the uropod exopod of his fourth stage; this is a feature of third stage zoeae of the present material, whereas 7 setae are present in all fourth stage specimens studied. The absence of setae on the maxilla scaphognathite posterior margin and the presence of 10 setae on the anterior part (compared with the 14 present in the fourth stage of the present material) suggests that Sars' figure of this appendage may represent a third stage zoea.

The slight differences noted between the present material and the brief descriptions of the larval stages of *A. chiroacanthus* by MacDonald *et al.* (1957) and Pike & Williamson (1959) perhaps reflect genotypic or phenotypic variability as their stages are undoubtedly correctly assigned and the average size at each stage of the present reared material from Millport agrees with the lower limit of the size ranges stated by these authors for the five larval stages. In their key to the identification of pagurid zoeae occurring in N.E. Atlantic waters, MacDonald *et al.* (1957) separate the zoeae of *Anapagurus* from those of other pagurids on the absence or the reduced posterio-lateral spine on abdominal segment 5 compared with the 'large lateral spines' on this segment in the other genera. In the reared material from Millport this posterio-lateral spine is well developed (see Fig. 17a) on segments 4 and 5 from the first to fourth zoeal stages. They were unable to find characters for separating the first zoeal stages of *A. chiroacanthus* from *A. hyndmanni* but used, as one of two features for distinguishing second stage zoeae of the species, the telson posterior margin 4th (ie 3rd plumodenticulate) seta which, in their material of *A. chiroacanthus,* was not longer than the 5th (ie 4th plumodenticulate) seta. However, second stage zoeae of the present material show some variability in this respect as some have this 3rd plumodenticulate seta noticeably longer than the 4th (see Fig. 3k) whereas in other specimens it ranges from being slightly shorter to subequal to the 4th on one half of the telson to slightly longer than the 4th on the opposite side. As mentioned previously, the fourth stage of the present material is without a pleopod bud on segment 4. The bud was present in this stage of *A. chiroacanthus* material studied by MacDonald *et al.* (1957) and was used, with other characters, for separating the fourth stage of this species from *A. hyndmanni.* The reduced or absent posterio-lateral spines on the fifth abdominal segment and the presence of an incipient pleopod 3 on segment 4 were also used in later revised keys by Pike & Williamson (1959: 1960) to separate zoeae of N.E. Atlantic/Mediterranean *Anapagurus* species from those of other pagurids. In these keys *A. chiroacanthus* is distinguished by having the rostrum projecting beyond the spine of the antennal exopod (scaphocerite) by about the length of the spine in the first and second stages and in having the innermost telson spine* shorter than either the 1st or 3rd plumodenticulate seta in the third and fourth stages. These are also features of the reared material from Millport. The partial regression of the first pair of pleopods noted in the two specimens studied of the second stage crab suggests that these may be males, although there is no evidence of gonopores or development of a coxal tube on the left pereiopod 5 characteristic of male *Anapagurus.* This assumption is based on the known state of pleopod development of later stage juveniles and also adults in which males have only uniramous second to fourth pleopods present on the left side of the abdomen; in females the first to fourth pleopods on the left side are biramous, although a uniramous pleopod 4 is occasionally present on the right side. Post-larval pleopod development has been studied in only a few pagurids. The first crab stage of *Clibanarius sclopetarius* Herbst and *C. vittatus* (Bosc), for example, has the left and right of the four paired pleopods equal in size (see Brossi-Garcia 1987*a*; 1988) whereas in *Dardanus pectinatus* (Ortmann) those on the right are smaller than those on the left (Forest 1954); a similar situation is just discernible in *Anapagurus chiroacanthus* (see Fig. 15a). In *Clibanarius,* sexual differentiation appears to occur only after the fifth stage crab. The pleopods are biramous and in the male the endopod remains small, but in females grows to equal the exopod length. Also, in the two species of *Clibanarius* mentioned the loss of pleopods from the right side of abdomen occurs through the second to fourth stages (Brossi-Garcia 1987*a*: 1988) whereas in *Clibanarius erythropus* (Latreille) they have disappeared by the second stage (Dechancé & Forest, 1958), a situation also apparent in *A. chiroacanthus.* By comparison, three pairs of symmetrical pleopods were reported as still present in a second stage crab designated *Anapagurus* species N.1 by Pike & Williamson (1960) and later assigned to *A. petiti* by Dechancé & Forest (1962). The occasional pairing of the fourth pleopods in adult females of *A. chiroacanthus* requires further study as it is not known whether the fourth pleopod on the right side is retained throughout post-larval development of this sex or is secondarily acquired at some later stage. Re-acquisition of pleopods (in this case the second pair) is known to occur in males of *Paguristes sericeus* A. Milne Edwards following their loss in the early juvenile stages (see Provenzano & Rice, 1964).

Provenzano (1971: 249) suggested there is '... great similarity between the described larvae of *Anapagurus, Catapaguroides, Orthopagurus* and the relatively large number of larvae of *Pagurus* so far described, although within the last genus, there is a diversity of forms ...' The larval development of *Orthopagurus* is known only from the brief account by Hart, (1937) of the terminal zoeal and megalopal stage of *Orthopagurus schmitti* (Stevens), whereas the complete larval development of *Cestopagurus* (previously *Catapaguroides*)

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* This process is termed '3rd telson spine' by Pike & Williamson (1959: 7). In this present study the processes on each half of the telson posterior margin are considered to be composed of: (i) an outermost furca, developed as a spiniform or cuspidate seta in *Anapagurus* but present as fixed spines in other pagurids; (ii) an adjacent pappose type seta; (iii) a number of plumodenticulate type setae. From the third stage the 2nd innermost plumodenticulate seta is replaced by a spine in many pagurids and is here designated as the 'innermost telson spine'.

timidus (Roux) was well described by Dechancé (1961). It appears possible to distinguish the terminal zoeal stage of *O. schmitti, C. timidus* and *A. chiroacanthus* using the following limited combined features:

Orthopagurus schmitti: (i) *carapace* posterio-lateral spine not produced but broadly angular; (ii) *telson* length about ×2 width, 2nd ?plumodenticulate seta on posterior margin longest and not developed as spine; (iii) *uropod* endopod without setae and exopod with several inner distal spines.

Cestopagurus timidus: (i) *carapace* posterior-lateral spine not produced, broadly angular; (ii) *telson* length about 1½× width and with 2nd plumodenticulate seta on posterior margin developed as spine and longest; (iii) *uropod* endopod with 1–2 setae and exopod without inner distal spines.

Anapagurus chiroacanthus: (i) *carapace* posterio-lateral spine small but produced, not broadly angular; (ii) *telson* lengh about 1½× width and with 2nd plumodenticulate seta on posterior margin developed as spine but not longest; (iii) *uropod* endopod with 1 seta and exopod without inner distal spines.

The detailed account by Dechancé (1961) of *Cestopagurus timidus* larval development enables satisfactory comparisons to be made with corresponding stages of *Anapagurus chiroacanthus* to which genus it may be phylogenetically closest. The zoeal stages of this species differ from those of *C. timidus* as follows: *Zoea I* (i) *antennule*: only 1 plumose seta present in *A. chiroacanthus* in addition to aesthetascs (*cf. 3* plumose setae in *C. timidus*); (ii) *maxillule*: endopod segment 3 with only 2 setae (*cf.* 3 setae), basis without plumodenticulate setae (*cf.* with setae); (iii) *maxilla*: basis with 4,4 (*cf.* 4,5); (iv) *maxilliped 1*: basis with a total of 8 setae on inner margin (distributed differently from those on this margin of *C. timidus* which has 10 setae), microtrichia present on outer margins of endopod segments 2–4 (not reported for *C. timidus*); (v) *maxilliped 2*: without mid-point seta on inner margin of basis (present in *C. timidus*), microtrichia present on outer margin of endopod segment 3 (not reported for *C. timids*); (vi) *telson*: posterior margin without median notch (*cf.* with notch). *Zoea II* (i) *antennule*: only one plumose seta present (*cf.* 2); (ii) *Maxillule*: basis with only one small simple seta (*cf.* 2 setae); (iii) *maxilla*: scaphognathite with 7 (*cf.* 8 setae) and coxa with 3,7 setae (*cf.* 4,7); (iv) *maxilliped*: 1 endopod inner margin segment 1 with 3 setae (*cf.* 2 setae); (v) *maxilliped* 3: endopod undeveloped (*cf.* developed and with 2 setae); (vi) *pleopod*-uropod: buds incipient (*cf.* not visible). *Zoea III* (i) *antennule*: only 3 plumose seta (*cf.* 6); (ii) *maxilla*: scaphognathite with 9 setae (*cf.* 8), basis with 4,5 setae (*cf.* 5,5); (iii) *maxilliped* 1: endopod inner margin of segment 1 with 3 setae (*cf.* 2); (iv) *maxilliped* 3: endopod bud without setae (*cf.* 2 setae); (v) *abdomen*: segment 5 posterio-lateral spines small (*cf.* larger); (vi) *pleopods*: endopods of uropods barely perceptible (*cf.* conspicuous buds); (vii) *telson*: with a pair of dorsal setae (*cf.* without dorsal setae), innermost telson spine about one fifth telson length (*cf.* one third) and anal spine absent (*cf.* present). *Zoea IV* (i) *maxillule*: coxa with 9 setae (*cf.* 8); (ii) *maxilla*: scaphognathite with 16 marginal setae, 4 on distal lobe (*cf.* 11 setae, none on distal lobe); (iii) *telson*: with 2 pairs of dorsal setae (*cf.* without setae), innermost telson spine about one ninth telson length (*cf.* one fifth telson length), anal spine absent (*cf.* present); (iv) *pleopod*: endopod of uropod with 1 seta (*cf.* 2 setae).

The megalopal stage of *Anapagurus chiroacanthus* can be distinguished from that of *C. timidus* (see Dechancé & Forest, 1958) in having: (i) *carapace*: of *A. chiroacanthus* with more acute rostral and subacute lateral projections; (ii) *eyes*: with proportionally longer eyestalks; (iii) *antenna*: with 10-segmented flagellum (*cf.* 7); (iv) *maxilla*: scaphognathite and basial endites with greater numbers of setae (25 marginal setae on scaphognathite and 8,7 on basis *cf.* 22 and 3,5); (v) *maxilliped* 2: exopod segment 2 with 6 setae (*cf.* 4) and endopod less developed i.e. (2-segmented *cf.* 5 segmented); (vi) *maxilliped* 3: exopod segment 2 with 8 setae (*cf.* 4); (vii) *pereiopod* 3: dactyl inner margin without spiniform setae (*cf.* 3); (viii) *pereiopod* 5; fewer pseudochaetal type setae on propodus; (ix) *pleopod* 4: only incipient (*cf.* well developed and with exopodal setae); (x) *pleopods*: endopod of uropod with one distal seta (*cf.* 3); (xi) *telson*: dorsal surface with 2 pairs of setae (*cf.* 3).

Of the numerous combined larval characters suggested by MacDonald *et al.* 1957 for distinguishing *Anapagurus* from those of *Pagurus,* only one, *viz.* less than 4 pairs of fully developed pleopods in the terminal zoeal stage and megalopa, can be considered exclusive for separating these two genera now that the larval morphology is known for a number of additional species of *Pagurus* (see Nyblade & McLaughlin, 1975 for references and also Tirmizi & Siddiqui, 1980; Hebling & Brossi-Garcia, 1981; Hong, 1981; Negreiros-Fransozo, 1984; Konishi & Quintana, 1987; McLaughlin & Gore 1988; McLaughlin *et al.* 1988). Features for separating the four groups of *Pagurus* larvae were reviewed by McLaughlin & Gore (1988: table I). Applying these to *Anapagurus* may allow the larvae of this genus to be distinguished from those of *Pagurus* on the following combined features. *Zoea*: (i) *carapace* of *Anapagurus* not elongated; (ii) *abdominal* segment 5 with short posterio-lateral spine, dorso-median spine on segment 6 absent; (iii) *telson* broad, '4th' (ie. 2nd plumodenticulate) seta developed as a spine from third zoeal stage and less than one half telson width; (iv) *Antenna*-endopod with 2 setae in ZI & II, exopod with curved outer margin, length less than ×3 width and with 9–10 setae; (v) *mandible*-palp absent; (vi) *pleopods* developed as buds only on segments 2 & 3 in stage IV zoea, uropod endopod with 1 seta. *Megalopa*: (i) *antenna*-flagellum reaching to or just beyond extremities of chelipeds; (ii) pleopods fully developed only on segments 2–4; (iii) *colour*-yellow chromatophore over stomach present.

It is not easy to distinguish plesiomorphic from apomorphic characters of pagurid larvae. Meristic studies of *A. chiroacanthus* suggest that the zoeae of this species are less plesiomorphic than *C. timidus* if reduction of setal numbers and their types on limb endites implies a more derived state. Whereas features such as the presence of telson dorsal setae, the retention of furcal spiniform/cuspidate setae (see below), the developed setae on the scaphognathite posterior margin and the relatively shorter innermost telson spines may be apomorphic characters of *A. chiroacanthus* zoeae. However, the megalopa of *A. chiroacanthus* has slightly greater numbers of setae and the antennal flagellum has more segments when compared with *C. timidus* but this condition may reflect the slightly larger overall size of *A. chiroacanthus* megalopa. Many other features of *A. chiroacanthus* megalopal stage (i.e. absence of spiniform setae on inner margins of dactyls of second and third pereiopod; fewer pseudochaetal type setae on propodal surface of the fifth pereiopod; fourth pleopod only incipiently developed and uropod endopod with only one seta; dorsal surface of telson with two pairs of setae) perhaps suggests a more derived condition that obtains for the related *C. timidus*, but it is debatable if all these features are truly apomorphic.

The types of setae on the body and limb endites of larval pagurids has received scant attention. The terminology used in this study to classify setae on *A. chiroacanthus* follows the schemes proposed by Drach & Jacques (1977) and Pohle & Telford (1981) with the exception of subdivisions of the plumodenticulate categories proposed by the latter. The types of setae noted on body surfaces and appendages are mentioned in the descriptive account (p. 00) and aspects related to ontogeny are noted here. The transformation of one type of seta into another or the replacement of one type by another is particularly evident at the moult from terminal zoeal stage to megalopa. For example, this change is obvious when setae on the telson posterior margin of the last zoeal stage and megalopa are compared. These change from a stout zoeal plumodenticulate type into a thin megalopal plumose type, accompanied by the total disappearance of the telson spiniform/cuspidate furcal setae and the adjacent (pappose) seta. The telson furcae are developed as spiniform/cuspidate setae in all zoeal stages of *A. chiroacanthus* as correctly shown by Sars (1890), but not by MacDonald *et al.* (1957) who illustrate these processes as fixed spines. However, fixed furcal spines are recorded as present throughout the zoeal development of a number of pagurids e.g. *Paguristes, Petrochirus, Diogenes, Cestopagurus* and some *Pagurus* species (see Rice & Provenzano, 1965; Provenzano, 1968; Baba & Fukuda, 1985; Dechancé, 1961; Nyblade & McLaughlin, 1975: 286; Hong, 1981; MacLaughlin *et al.* 1988 & MacLaughlin & Gore, 1988). By comparison, these furcal processes of other pagurids appear to be developed as spiniform setae in all stages e.g. *Clibanarius, Labidochirus, Calcinus, Pylopaguropsis, Phimochirus* and some *Pagurus* species (see Lang & Young, 1977; Nyblade & McLaughlin, 1975; Provenzano, 1962; Provenzano, 1971; Gore & Scotto, 1983). But for one species, *Lithopagurus yucatanicus,* there is a suggestion that the furcal spines become transformed into setae in later stages (see Provenzano, 1968*a*, Fig. 7). The transition of the '3rd' (i.e. 2nd plumodenticulate) telson seta into a spine occurs in the late zoeal stages of many pagurid species having either furcal spiniform setae or furcal spines, whereas in a more limited number the '3rd' telson seta is never replaced by a spine and this feature may be indicative of an apomorphic condition, as suggested by Gore & Scotto (1983).

The transformation of the maxillule basis from a narrowed endite bearing stout cuspidate setae in the zoea, to a broad endite armed with small spiniform setae in the megalopa, and the total disappearance of the stout plumose setae and their replacement by simple setae on the antennal exopod during the moult from terminal zoeal stage to megalopa, are also examples of setal transformations. Less obvious, perhaps, is the replacement of the simple seta adjacent to the antennal exopod disto-external spine, with a plumose type during the moult from first to second stage zoea. This type of change occurs also in the development from first to second stage of other pagurids e.g. *Cestopagurus timidus* (Dechancé, 1961), *Calcinus tibicens* (Provenzano, 1962), *Pagurus alatus* (Bookhout, 1972), and *P. dubius* (Hong, 1981) but is clearly not the case for others. Finally, a feature worth noting is the maximum number of sub-distal setae acquired on the ventral surface of the zoeal maxillule basis. These are absent in all stages of the Millport reared material of *A. chiroacanthus* and may be absent also in some species of *Pagurus* (e.g. they are not shown in figures of the maxillule of *Pagurus maclaughlinae* by MacLaughlin & Gore 1988). Only one seta occurs in *Diogenes nitidimanus* (Baba & Fukuda, 1985), *Pagurus prideaux, P. alatus* and *P. variabilis* (Goldstein & Bookhout, 1972; Bookhout, 1972; Samuelsen, 1972) whereas two are present in many other pagurids.

ACKNOWLEDGEMENTS. I wish to thank Miss P. L. Cook and Mr P. J. Chimonides for making available the ovigerous specimens of *A. chiroacanthus* on which this study is based, Dr A. L. Rice for his comments on the manuscript and Don Claugher for his assistance with the preparation of material for the scanning electron microscope studies.

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Manuscript accepted for publication 6 September 1989.

Bull. Br. Mus. nat. Hist (Zool.) **56**(2): 135–143 Issued 25 October 1990

Redescription of *Martialia hyadesi* Rochebrune and Mabille, 1889 (Mollusca: Cephalopoda) from the Southern ocean

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SYNOPSIS. *Martialia hyadesi* Rochebrune & Mabille, 1889 is redescribed from material obtained aboard commercial squid jigging vessels at the Antarctic Polar Frontal Zone, in the vicinity of South Georgia, and on the Patagonian Shelf. The new material confirms the position of the species in the sub-family Todarodinae and indicates a closer affinity with the genus *Todarodes* than *Nototodarus*. Distribution is related to the cool, temperate waters of the Southern Ocean and Antarctic Polar Frontal Zone. It is known to occur in the South Atlantic and western Pacific sectors of the Southern Ocean.

INTRODUCTION

Rochebrune & Mabille (1889) first described the ommastrephid squid *Martialia hyadesi*, somewhat briefly, from a single specimen taken at Orange Bay, Cape Horn in 1882. Further data from the type specimen were later reported by Wormuth (1976), but this specimen was in too poor a condition for a full redescription to be made, or for it to be illustrated. Further material was collected in the region of the Falkland Islands in 1966 and described by de Castellanos (1967). A mass stranding of the species occurred at Macquarie Island in 1971 (O'Sullivan *et al.*, 1983) and Nesis & Nigmatullin (1972) report its presence in the Patagonian Shelf area and illustrate the hectocotylus and spermatophore.

Martialia hyadesi has recently been recorded as a minor by-catch in the fishery for *Illex argentinus* on the Patagonian Shelf (Anon., 1989). In 1986 it contributed some twenty six thousand tonnes to the total catch of this fishery (Masutomi, Pers. comm.) and a substantial collection of frozen and formalin fixed specimens was obtained for study.

Comparison of this material with mandibles and soft parts from the regurgitations and gut contents of wandering and grey-headed albatross (*Diomedea exulans* and *D. chrysostoma*) chicks from Bird Island, South Georgia revealed that *Martialia hyadesi* is an important component of the cephalopod diet of these birds, especially the grey-headed albatross (Rodhouse *et al.*, 1987; Rodhouse *et al.*, 1990). Comparison with earlier material from grey-headed albatross and black-browed albatross (*D. melanophris*) at Bird Island, provisionally identified by Clarke & Prince (1981) as *Todarodes* (?) *sagittatus*, revealed that this was also *Martialia hyadesi* (Rodhouse *et al.*, 1990). It therefore became apparent that the species is ecologically important in the sub-Antarctic waters of the south Atlantic and is also a potential candidate for commercial exploitation in the region (Rodhouse, in press).

In 1989 two Japanese fishing vessels, equipped with squid jigging gear (Hamabe *et al.*, 1983), carried out commercial fishing trials in the vicinity of South Georgia and caught some 8 tonnes of *Martialia hyadesi* at the Antarctic Polar Front Zone to the west of the island. These trials were observed by British Antarctic Survey scientists and a further collection of frozen and fixed *M. hyadesi* was made. These two collections thus provided an opportunity to examine a large sample of well preserved specimens from two areas separated by a distance of some 1000 km. In view of the ecological and commercial importance of *M. hyadesi* in the Southern ocean we give here a full redescription of the species based on both the type specimen and the new material. The original brief description was based on a single specimen. This redescription gives a fully illustrated account of both sexes and includes quantitative data from a size range of specimens.

Specimens from these collections have been deposited at The Natural History Museum (BM(NH)), London, the Royal

Scottish Museum, Edinburgh (NMSZ 1990005), the Museum National d'Histoire Naturelle, Paris, and the Smithsonian Institution, Washington D.C. (USNM 817585).

MATERIALS AND METHODS

Samples of *Martialia hyadesi* were taken aboard a commercial Japanese squid jigging vessel, 'Showa Maru No. 23', on the Patagonian Shelf between 7 and 26 March 1986 within a rectangle 46° 17′S to 49° 48′S and 059° 27′W to 060° 58′W. Further samples were obtained aboard two jigging vessels, 'Seishu Maru No. 26' and 'Zenpo Maru No. 61' at the Antarctic Polar Frontal Zone between 9 and 10 February 1989 within a small rectangle 52° 42′S to 52° 45′S and 047° 01′W to 047° 04′W.

Samples from both areas were divided and some specimens fixed in 5% formaldehyde in seawater and others frozen at −20°C. Both fixed and thawed specimens were examined subsequently at the British Antarctic Survey's laboratories in Cambridge. Illustrations of the whole squid, most soft parts, beaks and the statolith were prepared using thawed material. Sucker and gill lamellae counts and the illustrations of the funnel organ and spermatophore were prepared from formalin-fixed material.

Definitions of characters and indices are taken from Roper & Voss (1983) and Roper *et al.* (1984), an index of a character being the ratio of its length to the mantle length expressed as percentage. Definitions of detailed features of the beak are taken from Clarke (1986) and of the statolith from Clarke (1978). Measurements were made on a total of seventy thawed specimens; thirty-five each from the Patagonian Shelf and Antarctic Polar Frontal Zone. All linear measurements of characters were made to the nearest 1.0 or 0.1 mm. Samples were weighed on a top loading balance to the nearest g. Sexual maturity was assigned to specimens according to the scale given by Lipinski (1979).

The type specimen of *Martialia hyadesi* was obtained on loan by kind permission of the Museum National d'Histoire Naturelle, Paris. It has a mantle length of 302 mm which falls within the range (216–319 mm) of the new material reported here. The poor condition of this specimen dictated that no additions to previous descriptions could be made, but the characters in the new material, described below, were examined with reference to the type where possible.

REDESCRIPTION AND RESULTS

Synonomy

Martialia hyadesi Rochebrune and Mabille, 1889, pp. 9–10, pl. 1 (type: Orange Bay, Cape Horn; Museum Nationale d'Histoire Naturelle, Paris)
Ommastrephes hyadesi Pfeffer, 1912, p. 451
Ommastrephes hyadesi Dell, 1952, p. 119

A label with the type specimen records that it was collected at Cook Bay, not Orange Bay as given by Rochebrune & Mabille (1889). Also the date of publication given by these authors with the original description is 1887. However, the work was not published until 1889 which is thus the valid starting-point date.

Description of characters

MANTLE. Powerful, robust, cylindrical for most of length, tapering slightly towards point of insertion of fins, then tapering abruptly to a somewhat elongated tail. Dorsal margin at anterior opening extends to a low point; ventral margin slightly excavated below funnel (Fig. 1a, c). Mantle of type in poor condition but agrees with new specimens.

GLADIUS. Strong, elongate; rachis reinforced with one central and two lateral ribs; vane extends less than one fifth total length of gladius; conus extends less than one seventh length of vane (Fig. 1b). Conus on type appears to have unfurled during preservation but otherwise agrees with new specimens. However, a note by M. Roeleveld with the gladius accompanying the type suggests that this may belong to another specimen.

FINS. Extend about two fifths length of mantle. Approximately rhomboidal; posterior edge, which is concave for most of length, is longer than anterior edge which is convex; lobes at point of insertion of anterior edges with mantle (Fig. 1a, c). Fin angle: 47–55°, slightly larger than the type specimen's fin angle of 45°.

HEAD. Slightly narrower than width of mantle opening (Fig. 1a, c). Three prominent nuchal folds on each side; one above level of eye, one approximately level with middle of eye, one below level of eye. These are poorly preserved in the type but agree with the new specimens on the left side of the head. Width of head variable in thawed material due to variation in quality of preservation of eyes.

FUNNEL. Strong, broadly conical, extending to approximately middle of eye. Funnel valve a flap close to funnel opening. Funnel organ with a 'V' shaped dorsal member, apex pointing anteriorly, and two ovoid ventral members (Fig. 2a). Funnel groove deep with foveola possessing seven longitudinal folds. These were not apparent and could not be counted in thawed specimens but were prominent in formalin fixed material (Fig. 2b). No side pockets. All features of funnel in new specimens agree well with the type.

FUNNEL MANTLE LOCKING CARTILAGE. Strong, typical ommastrephid inverted 'T' shape (Roper *et al.*, 1969); straight, simple, longitudinal groove, straight mantle component (Fig. 2c). Apparently identical to type.

ARMS. Moderately robust and less than half length of mantle. Arms I and IV approximately equal in females and shorter than arms II and III which are also approximately equal. Hectocotylised right arm IV shorter than arm I in males (see below). Swimming keel well developed on proximal half of arm III. Cross sections of arms roughly ovoid or rounded triangular in central part. Protective membrance poorly developed; trabeculae strongly developed and prominent. Relatively small arm suckers in biserial longitudinal rows; largest suckers on central part of arms; each sucker associated with a trabeculum so there are equal numbers of each. Transverse rows oblique (Fig. 3a). Depending upon sucker size, rings armed with 5, 7 or 9 teeth which occupy more than half circumference on distal edge. Central tooth generally slightly larger than lateral teeth; shape asymmetric in some suckers (Fig. 3c). Arm sucker counts for a sample of

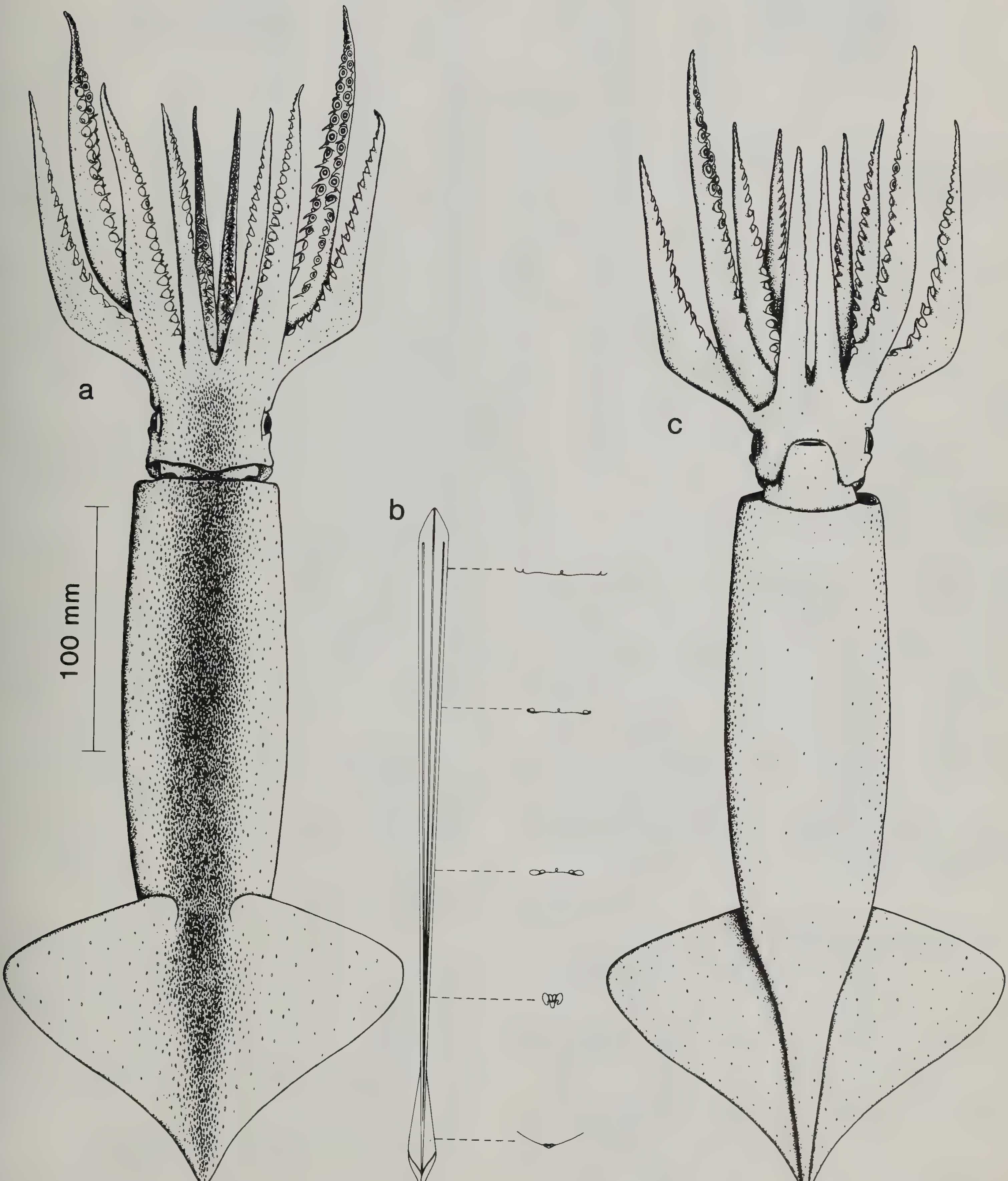

Fig. 1 *Martialia hyadesi*: a) dorsal view, b) gladius showing sections depicted dorsal side down, c) ventral view.

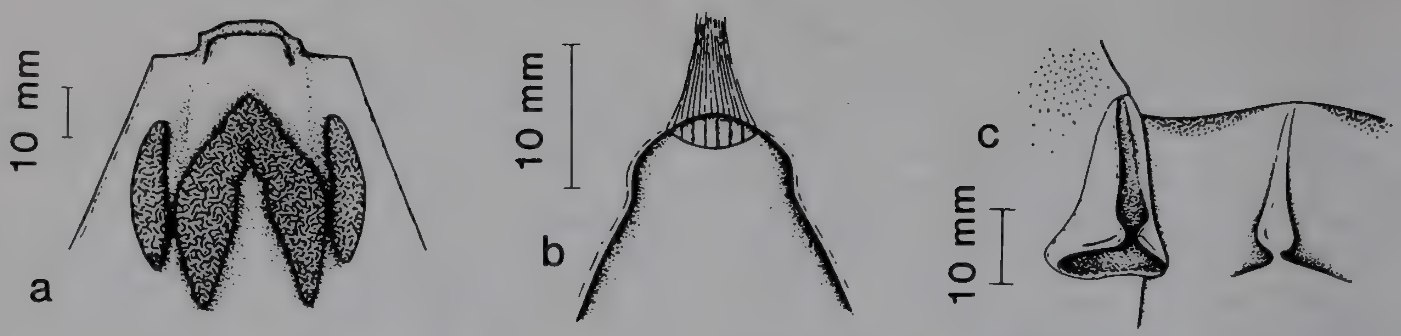

Fig. 2 *Martialia hyadesi*: a) funnel organ, b) funnel groove, c) funnel locking-cartilage.

Table 1 Sucker counts on the arms and tentacular club of *Martialia hyadesi*: new specimens and the type

	New specimens				Type specimen
	Range	Mean	±sd	n	
Arm I	66–82	75.3	4.5	11	66
II	67–87	74.7	5.3	11	72
III	66–78	74.0	4.3	11	70
IV (Female)	74–84	78.0	5.3	3	74
Carpus	17–21	19.3	2.1	3	20
Manus	88–93	90.0	2.6	3	92
Dactylus	42–48	45.3	3.1	3	48

new specimens, and the type, are given in Table 1. The arms and arm sucker counts agree with the type.

HECTOCOTYLUS. On modified right arm IV which is somewhat shorter and thicker than unmodified, or slightly modified, left arm IV. In stage III, preparatory, and stage IV, maturing males, proximal part of modified arm is similar to unmodified arm with two rows of suckers; each sucker associated with a trabeculum and with largest suckers on central part of arm. At distal end, arm becomes modified, suckers much smaller than on unmodified arm. Hectocotylus occupies distal third of right arm. On ventral side trabeculae are disassociated from the suckers at stalk base and form rounded flaps; on dorsal side trabeculae become reduced towards end of arm and are absent on hectocotylised part (Fig. 3b). Slight modification of left arm IV of males limited to elongation of sucker stalks on distal third of arm (Fig. 3b). No comparison could be made with the type which is female.

TENTACLE AND CLUB. Tentacle length greater than half length of the mantle; most of tentacle occupied by club which is not expanded and is rounded/triangular in cross section. Protective membrane poorly developed; trabeculae strongly developed, prominent. Club not clearly differentiated into carpus, manus and dactylus (Fig. 3a); its structure is interpreted here according to the scheme given by Roeleveld (1982) for other ommastrephids. No fixing apparatus. Approximately 7–9 paired finger-like projections present at proximal end of carpal area. On rest of carpal area suckers arranged in biserial longitudinal rows, each sucker attached by a stalk to base of a trabeculum, as on arms. Transverse rows oblique. Dentition of ten or so pairs of suckers on carpal area resembles that on arm suckers, usually seven teeth occupying more than half circumference on distal edge of sucker ring (Fig. 3c). On manus area suckers arranged in tetraserial longitudinal rows: outer rows consist of small suckers attached by stalks to bases of trabeculae as on arms; inner rows consist of larger suckers attached by stalks to central part of club. Dentition on these suckers usually consists of fifteen relatively large, sharp teeth alternating with fifteen smaller, flatter teeth or plates which together occupy entire circumference of ring; teeth, and especially plates, larger on distal edge. On largest manus suckers one tooth is larger than rest, but extent of enlargement is variable (Fig. 3c). On dactylus area, small suckers arranged in tetraserial longitudinal rows, trabeculae reduced, low protective membrane better developed on the ventral side. Dentition of suckers on dactylus area similar to that on manus area (Fig. 3c). Well developed keel on distal third of club. Sucker counts for the carpus, manus and dactylus areas of club are given in Table 1. Tentacle and club on new specimens agree with the type.

BUCCAL MASS. Buccal membrane formula: DDVD (Fig. 3a) in new specimens and type.

BEAK. Lower beak possesses typical ommastrephid features: a shoulder which forms a tooth, a transparent strip below jaw angle, a low wing fold, a broad hood with a notch and a long rostral edge approximately equal to length of hood in midline (Clarke, 1986). No fold in lateral wall and rostrum characterised by a pronounced hook (Fig. 4a). Keratinisation tends to be blacker than in most other ommastrephid beaks (Fig. 4a, b). Darkened patch on wing of more mature specimens. Beak not removed from type but shape of rostrum, which could be examined, agreed well with new specimens.

The calculated regression of lower rostral length (r) in mm against wet weight in grams (w) is:

$$\ln w = 2.405 + 2.012 \ln r \ (r^2 = 0.756;\ n = 67)$$

and against mantle length in mm (l) is:

$$l = 102.0 + 29.47\, r \ (r^2 = 0.736;\ n = 67)$$

RADULA. Lateral tooth row contains a rhachidian tooth, three pairs of lateral teeth and a pair of marginal plates. Heterodont, first and second teeth similar in size to rhachidian, third lateral teeth long and sharply pointed, marginal plates poorly developed but usually visible, especially under polarised light. A small cusp on each side of base of rhachidian tooth; a single cusp on outer edge of base of first lateral tooth (Fig. 4c). Radula of type not examined.

GILLS. Gill lamellae counts fell in the range 61–67 (mean: 64.8 ± 2.7; n = 6). Gills of type not examined.

SKIN AND CHROMATOPHORES. In live specimens skin on dorsal surface of mantle smooth and has a very dark and dense

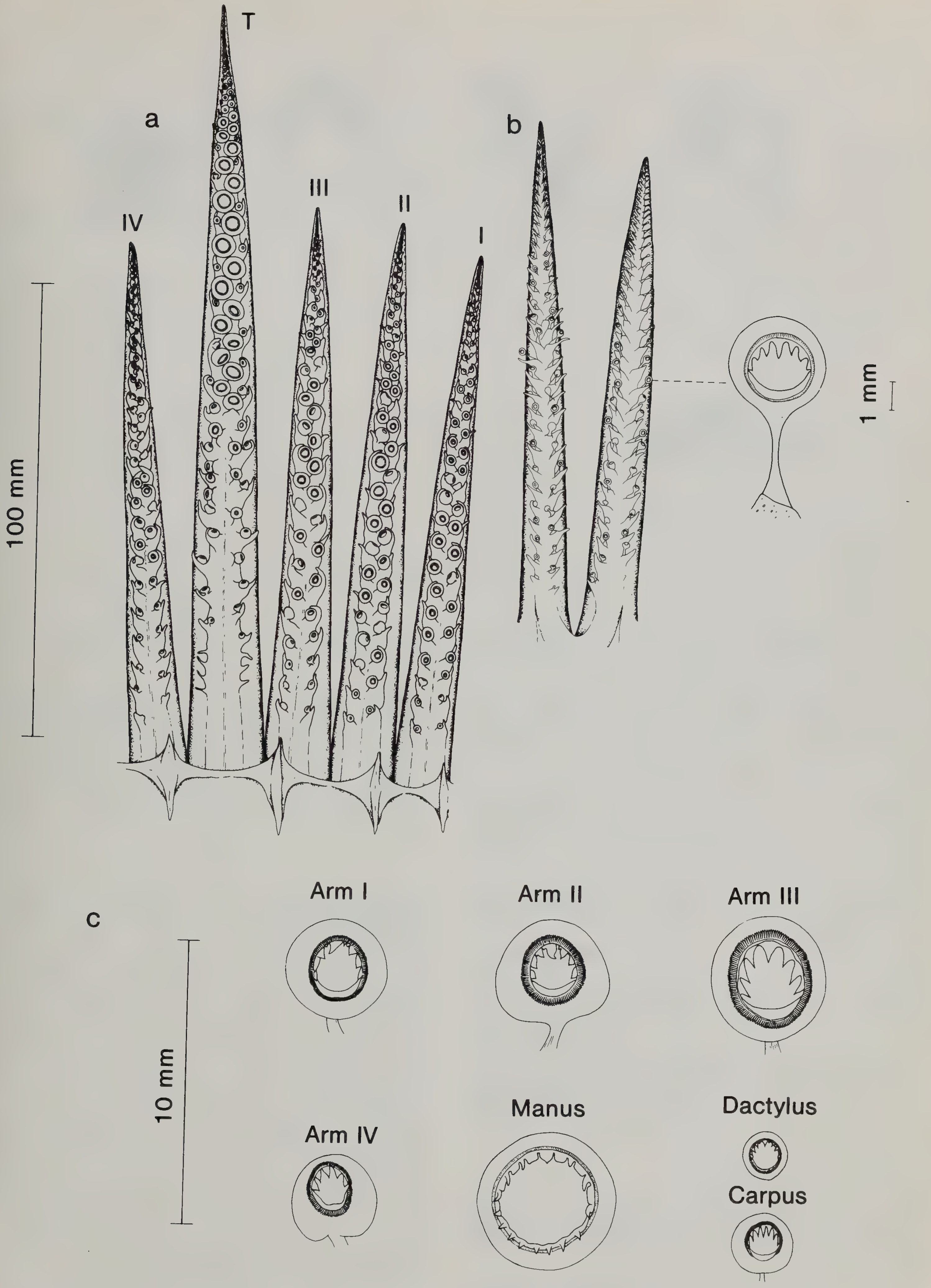
a
T
IV
III
II
I
100 mm
b
1 mm
c
10 mm
Arm I
Arm II
Arm III
Arm IV
Manus
Dactylus
Carpus

Fig. 3 *Martialia hyadesi*: a) right arms and tentacle, b) male arms IV showing hectocotylised right arm, c) largest sucker from each arm and tentacular club region.

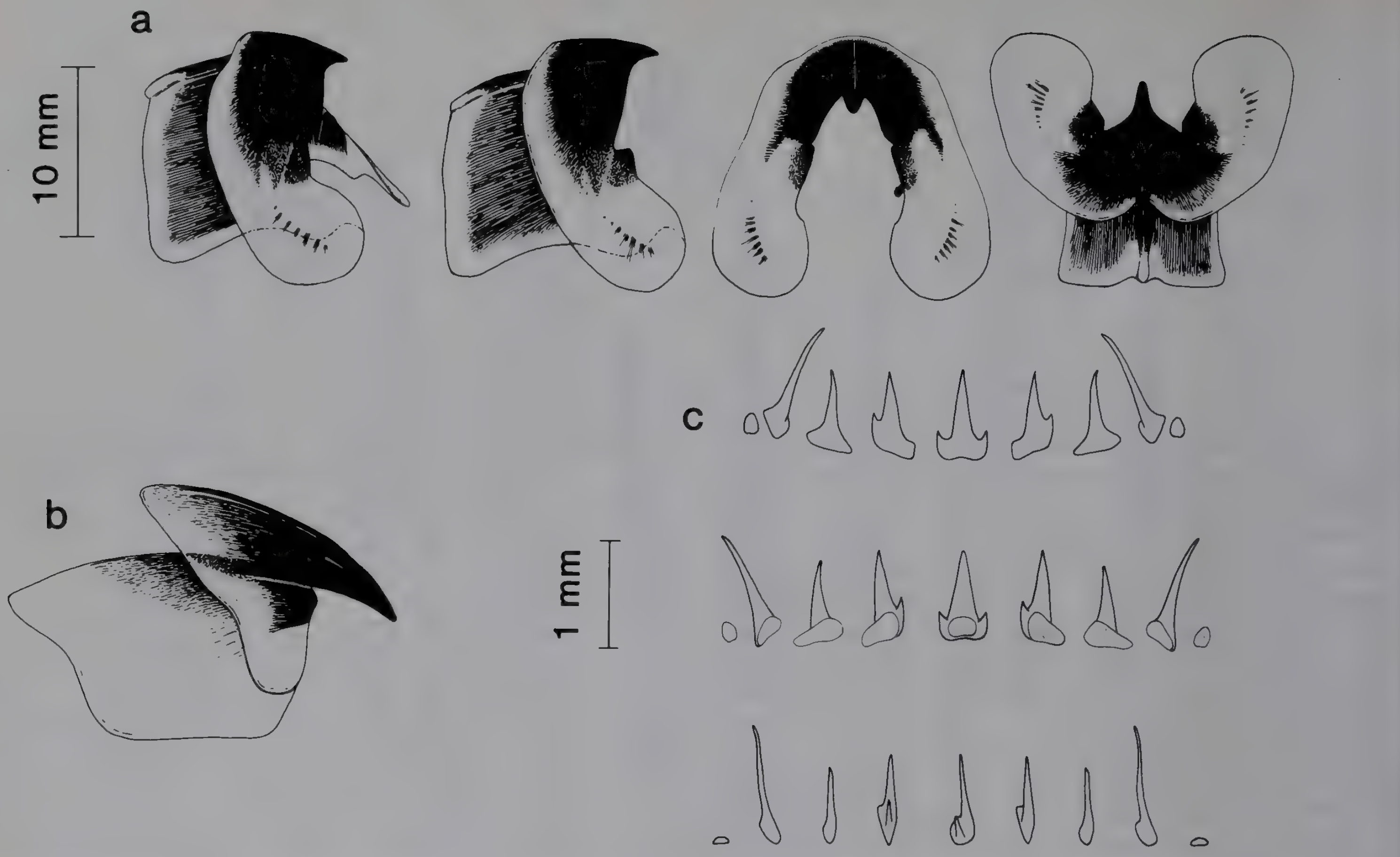

Fig. 4 *Martialia hyadesi*: a) lower beak, b) upper beak (drawn to some scale as lower beak), c) tooth row on the radula (top: oral view; middle: rotated 180°; bottom: rotated 90°.

purple colouration. Laterally this becomes red/brown and ventrally the skin is silver/white. Pronounced red patch on head above eye. Chromatophores small. A colour photograph of a live specimen from the Patagonian Shelf is given by Rodhouse (1989).

No photophores were found on the skin or elsewhere.

Skin of type has deteriorated and no useful comparison could be made with new specimens.

SPERMATOPHORES. Elongate and slender. A mature spermatophore is illustrated in Fig. 5a. No comparison could be made with the type which is female.

STATOLITH. All statoliths examined were adult stage (Morris and Aldrich, 1984). Seen from the anterior side (Fig. 5b) the dorsal dome is large and virtually indistinguishable from the lateral dome; no distinct lobes on the lateral dome or rostrum. Tip of rostrum flexed anteriorly; rostral angle obtuse and approximately 150°. Dorsal and ventral indentation well defined; spur prominent forming a distinct protrusion on the anterior surface. No obvious anterior ridge. Medial fissure present. Statoliths of type not examined.

Measurements and indices

All measurements of characters are given in the appendix. Mean (±sd) and range of calculated indices are given in Table 2 together with data for the type specimen taken from Wormuth (1976).

Comparison of the character indices for the type specimen of *Martialia hyadesi*, with data for the new material (Table 2), shows that the type specimen falls within the range for all indices calculated for the new material, apart from MWI and HLI. Mantle width is a low precision measurement (Wormuth, 1976) and in any case the MWI for the type specimen was only slightly less than for the present material. The head length of the type specimen is apparently somewhat longer relative to the mantle length than the longest head measured in our recent collections.

DISCUSSION

The specimens described here, which are indisputably *Martialia hyadesi* on the basis of the above comparisons, confirm the position of the species within the sub-family Todarodinae on the basis of the funnel groove, which has a foveola but no side pockets, and because of the absence of photophores (Roper, Young & Voss, 1969). The sub-familial position is also confirmed on the alternative basis of the ventral distal development of the trabeculae on the hectocotylus (Roeleveld, 1988). The genus *Martialia* (de Castellanos, 1967) is distinguished from the other genera of the sub-family by two features: 1) the tentacular club which extends almost to the base of the tentacle, is not expanded—an atypical feature in the Ommastrephidae (Young & Roper, 1968)—and possesses a biserial row of finger-like projections on the proximal part; and 2) well developed trabeculae, associated with a reduced protective membrane, on the arms and tentacles (Roper *et al.*, 1984; Nesis, 1987).

In the males from the present collections only the right

Table 2 Character indices for male and female *Martialia hyadesi* (MWI: mantle width index; HLI: head length index; HWI: head width index; FLI: fin length index; FWI: fin width index; ALI I–IV: arm length indices, arms I–IV; HcLI: hectocotylus length index; TtTI: tentacle length index; CLI: club length index; GLI: gladius length index; GWI: gladius width index; RLI: rachis length index; RWI: rachis width index). Indices from the type specimen given by Wormuth (1976) are also indicated.

Character	Range	mean	±sd	Type specimen indices
Males				
MWI	19.0–29.7	23.4	2.1	
HLI	12.9–17.4	15.8	1.0	
HWI	12.0–18.4	15.5	1.4	
FLI	38.2–45.6	41.6	1.9	
FWI	54.3–66.5	60.0	2.8	
ALI 1	29.5–43.8	37.8	3.3	
ALI 2	34.6–48.8	41.5	3.0	
ALI 3	35.5–49.2	42.0	3.2	
ALI 4	27.7–36.5	32.5	2.3	
HcLI	6.6–14.9	10.5	2.3	
TtLI	49.3–66.9	58.6	4.7	
ClLI	38.2–55.6	48.4	4.1	
GLI	91.9–100.0	95.1	1.6	
GWI	2.8–4.7	3.3	0.4	
RLI	74.5–85.5	78.5	2.6	
RWI	3.8–4.7	4.3	0.2	
Females				
MWI	19.9–26.8	22.8	1.6	19.0
HLI	12.6–17.6	15.7	1.0	19.0
HWI	13.2–17.7	15.5	1.2	
FLI	38.4–45.5	42.0	1.8	43.0
FWI	55.5–64.3	59.4	2.3	55.5
ALI 1	29.9–43.2	36.9	2.8	37.0
ALI 2	35.2–45.7	40.4	2.7	41.0
ALI 3	35.7–46.1	40.9	2.6	43.0
ALI 4	30.1–40.8	35.2	2.6	37.0
TtLI	44.9–70.2	59.8	5.2	
ClLI	37.3–57.0	48.6	4.2	50.0
GLI	91.9–98.9	95.5	1.6	
GWI	2.6–3.7	3.1	0.2	
RLI	72.6–81.7	77.4	2.0	
RWI	3.9–5.0	4.3	0.3	

fourth arm is extensively modified to form a hectocotylus, which suggests a closer affinity with *Todarodes* than *Nototodarus*, in which both fourth arms are modified. However, the relationship between *Martialia* and *Todarodes* is not resolved and awaits further analysis (see Roeleveld, 1988).

Records for *Martialia hyadesi* presently exist from Cape Horn (Rochebrune & Mabille, 1889), Macquarie Island (O'Sullivan, 1983), the Patagonian Shelf, the Antarctic Polar Frontal Zone in the vicinity of South Georgia (this study), and from predators sampled at South Georgia (Hunter, 1983; Rodhouse *et al.*, 1987; Rodhouse *et al.*, 1990), Macquarie Island and Campbell Island (M. J. Imber, Pers. comm.). These records suggest that its distribution is related to the cool temperate waters of the Southern Ocean southwards to the Antarctic Polar Frontal Zone and possibly extending south of the Front. The sporadic appearance of the species in the Patagonian Shelf fishery suggests that it does not normally extend as far north as the Southern sub-Tropical Convergence. It is unclear whether its distribution is circumpolar or discontinuous. Imber & Berruti (1981) reported a single *Martialia hyadesi* beak among beaks from wandering albatrosses at Marion Island but none among beaks from sooty and light-mantled sooty albatrosses, *Phoebetria fusca* and *P. palpebrata*. Given the worn state of the beak (M. J. Imber, Pers. comm.) and the potential range of wandering albatrosses, this record does not confirm the occurrence of *M. hyadesi* near the Prince Edward Islands.

The distribution of *Martialia hyadesi* may overlap that of three other members of the family Ommastrephidae, *Todarodes filippovae* Adam, 1975, *Nototodarus sloani* (Gray, 1849) and *Illex argentinus* (de Castellanos, 1960), which are well described and illustrated (Roper *et al.*, 1984; Roper *et al.*, 1985). Complete specimens are unlikely to be confused with any of these. Beaks from gut contents and regurgitations of vertebrate predators should be readily identifiable as being from an ommastrephid and distinguishable from other species in the family (Clarke, 1986) by the narrow appearance, the presence of a distinctively hooked rostrum, a very low wing fold and the blackish keratin of the darkened areas.

Acknowledgements. We thank the fishing masters, captains and crews of the Japanese squid jiggers, Showa Maru no. 23 (KSJ), Zenpo Maru no. 61 and Seishu Maru no. 26 (OSA) for welcoming us aboard their vessels and for their assistance whilst at sea; Dr Ken Patterson (Falkland Islands Development Corporation) and Mr Tom Boyd (Witte Boyd Holdings Ltd.) for creating the opportunities to go to sea with the Japanese fishermen; Ms Emma Hatfield and Mr Mick Whitehouse for their help at sea; Dr Uwe Piatkowski and Mr Alistair Murray for their help in the laboratory and with statistical analyses; Dr Renata Boucher-Rodoni and Dr Philippe Bouchet for arranging the loan of the type specimen of *Martialia* from the Museum National d'Histoire Naturelle, Paris; Mr Susumu Masutomi, President, K.S.J. Corporation, 2–22–10, Misaki, Miura-City, Kanagawa-Ken, Japan, for information about the importation of *Martialia* to Japan; Dr Mike Imber and Prof. Malcolm Clarke for their advice and constructive criticism. Research at the British Antarctic Survey on cephalopods from the Patagonian Shelf area is funded by the Falkland Islands Government.

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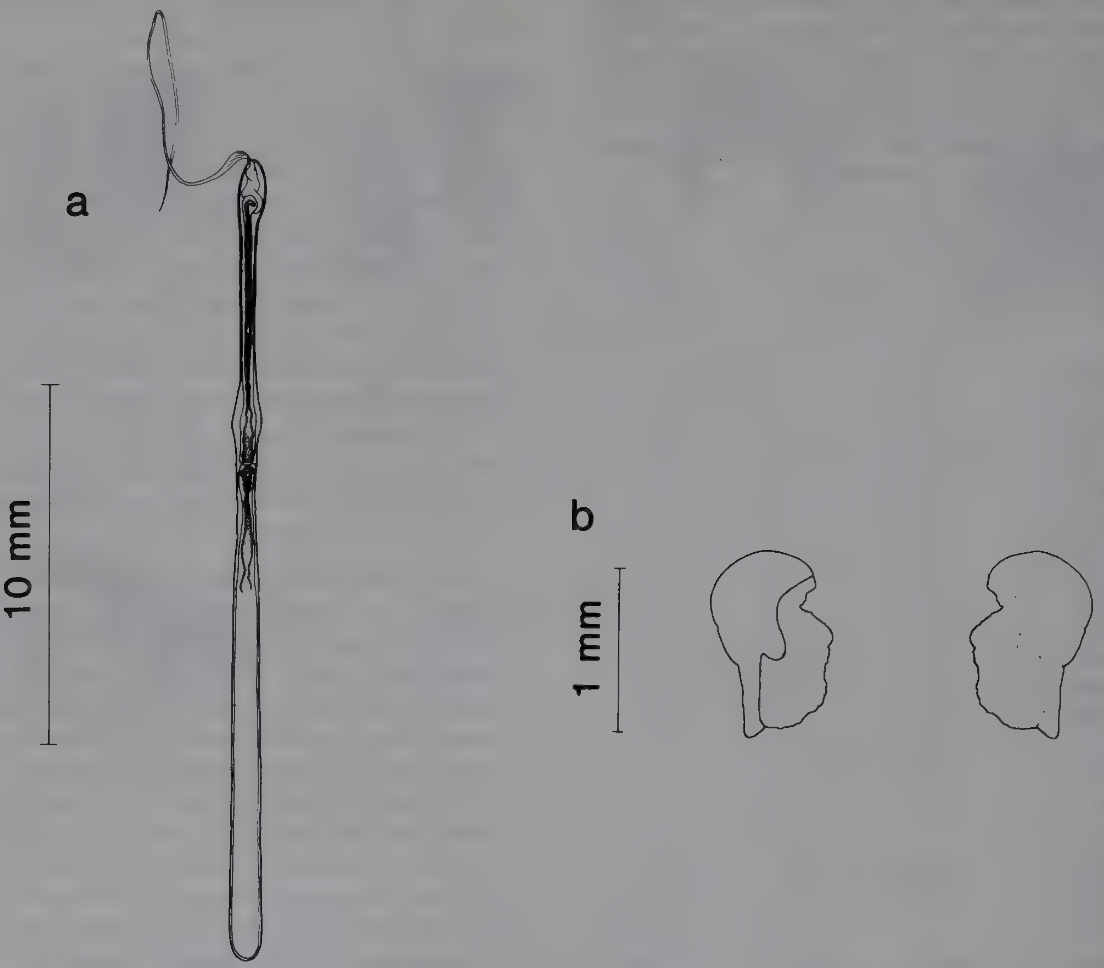

Fig. 5 *Martialia hyadesi*: a) spermatophore, b) right statolith: anterior side (i); posterior side (ii).

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Manuscript accepted for publication 23 January 1990

APPENDIX

Raw data from measurements of *Martialia hyadesi* from the Antarctic Polar Frontal Zone and the Patagonian Shelf (all measurements are in g or mm; S: sex; MS: maturity stage; TW: total weight; TL: total length; ML: dorsal mantle length; MW: mantle width; HL: head length; HW: head width; FL: fin length; FW: fin width; FA: fin angle; AL1: length arm I: AL2: length arm II; AL3: length arm III; AL4: length arm IV; HcL: hectocotylus length; TtL: tentacle length; CL: club length; GL: gladius length; GW: gladius width; RL: rachis length; RW: rachis width; LRL: lower rostral length).

Antarctic Polar Frontal Zone

S	MS	TW	TL	ML	MW	HL	HW	FL	FW	FA	AL1	AL2	AL3	AL4	HcL	TtL	CL	GL	GW	RL	RW	LRL
f	II	219	381	224	60	*	*	91	140	53	79	86	80	74	*	126	101	220	6	183	10	4.9
f	II	234	411	241	57	36	40	98	140	52	82	94	92	87	*	135	109	230	7	195	10	4.5
f	II	259	413	244	61	42	40	99	140	52	93	106	100	95	*	146	123	233	8	190	11	5.0
f	II	200	*	226	57	39	39	88	128	52	86	96	87	81	*	*	*	216	7	178	10	4.5
m	III	224	376	230	59	36	34	93	134	52	84	94	99	74	*	121	97	218	7	178	10	4.4
m	III	207	381	228	55	37	37	87	130	52	87	96	89	*	*	137	121	217	7	177	9	4.2
m	III	242	387	241	59	38	37	97	143	52	100	102	*	76	*	142	114	228	7	187	11	4.5
m	III	286	406	243	62	40	44	104	146	52	100	105	101	80	*	146	117	231	8	189	10	4.5
m	*	167	345	219	54	36	33	88	119	51	75	81	82	*	*	112	92	203	7	166	9	4.3
m	II	271	418	247	61	36	38	102	149	53	104	*	108	82	*	151	124	228	8	184	11	4.5
f	II	209	390	232	55	39	40	94	132	50	83	95	91	84	*	138	103	218	7	175	10	4.4
f	II	206	383	225	54	37	36	90	133	52	88	98	95	87	*	137	113	212	7	174	9	4.2
m	III	246	400	237	61	39	36	101	144	52	85	95	99	75	21	144	119	224	8	181	10	4.3
f	II	257	416	245	60	39	40	103	139	53	84	98	93	88	*	152	123	234	8	191	11	*
m	II	251	402	236	60	34	32	97	135	52	89	94	103	78	*	147	124	225	8	183	10	4.5
m	II	243	403	240	59	39	39	92	143	52	92	108	104	75	*	150	125	227	8	187	11	4.6
m	III	358	456	260	62	41	43	108	165	53	114	127	128	95	*	164	135	250	9	201	12	5.6
f	II	310	455	258	64	40	41	110	154	52	91	100	115	101	*	181	145	246	8	197	11	4.6
f	II	243	405	248	55	39	38	104	143	52	87	100	105	88	*	149	120	230	8	180	10	4.5
f	II	282	427	255	55	40	42	103	149	51	105	115	115	100	*	166	135	236	8	192	11	5.0
m	II	273	402	246	54	39	39	102	149	52	*	102	105	83	*	147	117	231	7	187	11	5.0
m	II	234	386	228	55	39	42	88	149	52	82	96	103	77	*	140	115	219	9	183	10	4.3
f	II	182	350	216	51	34	33	83	121	51	80	89	86	74	*	123	98	206	6	175	9	4.3
f	II	271	435	259	58	42	41	107	144	52	97	106	99	92	*	151	128	238	7	194	11	4.7
f	II	301	435	264	60	41	38	113	148	52	106	112	110	103	*	148	121	249	9	201	11	5.0
f	II	281	429	249	60	40	43	100	152	51	106	112	110	88	*	167	140	235	8	187	11	5.1
m	III	298	421	246	63	40	41	99	145	54	103	109	112	80	*	162	127	236	7	194	11	4.8
f	II	301	440	258	62	41	41	103	151	52	110	118	119	94	*	166	137	240	9	104	12	4.8
m	II	250	408	246	58	40	37	96	137	51	90	103	96	80	27	155	123	226	8	191	10	4.9
m	II	253	406	239	56	39	36	100	148	51	87	101	102	75	23	149	123	221	8	193	10	4.6
f	II	222	401	238	54	36	37	99	136	49	86	97	100	91	*	141	117	227	8	187	10	4.4
f	II	315	448	255	56	41	45	111	160	51	92	105	107	104	*	160	128	240	8	195	11	5.4
f	II	259	425	240	57	38	37	101	143	52	97	104	102	89	*	157	128	230	8	185	10	4.9
m	III	316	425	239	61	39	42	109	159	53	97	112	109	87	28	160	133	239	8	204	11	5.4
m	II	215	374	222	53	33	38	97	131	52	86	89	90	70	*	124	101	216	7	181	10	4.4

Patagonian Shelf

S	MS	TW	TL	ML	MW	HL	HW	FL	FW	FA	AL1	AL2	AL3	AL4	HcL	TtL	CL	GL	GW	RL	RW	LRL
m	III	242	*	242	46	38	36	103	139	50	83	95	97	73	29	*	*	234	7	190	10	4.7
f	III	442	*	295	63	43	44	125	175	51	115	118	121	101	*	*	*	286	10	230	13	6.0
f	II	385	463	285	57	36	38	121	168	52	101	107	113	94	*	148	126	271	8	221	11	5.8
f	II	392	488	278	62	46	46	116	164	50	102	111	116	95	*	165	133	269	9	215	13	5.9
f	II	210	369	236	47	34	32	93	131	47	79	84	86	71	*	106	88	223	7	186	10	*
f	II	245	408	248	52	38	36	106	150	52	79	88	92	78	*	135	104	239	8	195	10	5.1
f	III	575	535	298	74	47	41	115	189	55	109	130	128	110	*	194	164	290	10	235	15	6.1
f	III	505	524	297	68	50	50	129	183	51	108	129	135	110	*	192	142	288	9	229	13	6.2
f	III	527	*	302	72	53	48	124	176	52	*	115	123	105	*	*	*	292	9	236	13	6.1
m	IV	464	505	286	57	44	42	125	173	53	106	121	120	101	36	177	151	275	9	223	13	5.7
f	II	344	446	265	57	43	44	114	166	49	99	103	104	85	*	151	132	254	8	203	12	6.1
m	III	239	403	241	47	36	36	105	145	51	92	99	108	74	16	140	123	230	8	188	10	5.5
m	III	330	424	258	56	45	43	105	157	52	94	104	106	89	34	131	117	245	8	204	11	5.9
f	II	295	435	260	56	39	41	112	154	51	98	105	116	87	*	152	124	251	8	198	11	5.4
f	III	503	521	300	68	47	46	135	193	50	116	127	129	105	*	210	171	285	9	226	14	6.6
f	II	331	455	274	64	41	40	112	161	47	94	99	105	89	*	161	130	263	8	211	11	6.0
m	IV	433	466	281	59	38	38	122	173	51	108	114	114	87	34	163	132	267	9	215	12	5.8
f	II	422	486	271	64	46	43	116	173	52	117	119	119	105	*	183	154	268	10	217	12	6.2
f	III	401	475	279	59	46	44	115	166	52	102	105	108	94	*	162	131	266	9	215	12	5.6
m	III	282	434	263	50	40	37	114	156	52	*	105	95	*	*	138	119	249	8	202	11	5.5
f	II	255	419	249	60	40	35	110	152	50	90	98	96	77	*	140	118	*	8	*	*	5.3
f	II	342	446	266	64	41	35	118	155	49	96	104	105	86	*	137	112	263	7	211	11	5.8
m	III	290	423	235	59	37	33	98	151	*	102	109	112	84	35	138	118	*	11	201	11	5.6
f	II	338	450	266	59	41	39	113	163	49	98	110	106	89	*	155	124	255	8	212	11	6.0
f	III	658	562	319	67	50	52	145	198	50	110	121	128	106	*	179	151	302	10	238	14	6.9
f	III	493	508	295	64	43	40	134	176	49	112	114	114	105	*	186	152	280	10	221	13	6.4
m	IV	508	486	*	59	48	45	122	165	51	106	111	113	86	36	150	125	275	9	219	12	6.1
f	II	377	484	281	58	42	38	125	164	50	84	99	*	88	*	160	130	266	9	216	12	5.7
f	III	437	474	269	60	45	43	118	160	50	98	112	110	90	*	172	137	258	10	210	13	5.7
f	II	358	460	269	59	35	39	118	161	51	100	111	119	101	*	166	132	255	8	213	12	5.7
m	II	169	343	217	43	28	26	89	120	52	64	75	77	58	18	107	83	208	7	171	9	4.2
m	III	327	445	258	63	44	43	117	157	51	88	104	103	74	22	140	111	246	9	195	12	4.6
m	III	243	395	236	55	36	35	98	144	52	83	92	99	78	20	136	110	225	8	187	9	5.1
f	II	443	475	288	58	42	40	122	171	50	101	105	112	96	*	162	137	281	9	230	14	*
m	II	208	363	224	51	37	36	93	138	52	81	88	92	74	22	120	102	212	7	184	10	5.0

Bull. Br. Mus. nat. Hist (Zool.) **56**(2): 145–153 Issued 25 October 1990

The phylogenetic relationships of salmonoid fishes

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Introduction

The family Salmonidae (salmons, trouts and charrs) have long been of scientific interest, primarily because of their economic significance but also because their phylogenetic relationships to other teleost groups have proved difficult to ascertain. As currently defined, the family comprises three subfamilies, *viz* Salmoninae (salmons and trouts), Thymallinae (graylings) and Coregoninae (charrs and whitefishes). The Salmonidae have been regarded as a relatively primitive teleost group since they have supposedly retained many features often associated with so-called 'primitive' groups. Such features include; soft fin-rays; adipose fin; oviducts absent or incomplete and three upturned caudal vertebrae. This view is perhaps misleading as the Salmonidae possess many unique characteristics particularly with regard to their physiology and reproductive strategies.

The Salmonidae are native throughout the Holarctic region but are absent from tropical and austral regions. Some species (e.g *Salmo trutta* and *Oncorhynchus mykiss*) have, however, been introduced into these regions (Scott & Crossman, 1973:186). The original distribution of some salmonid species is difficult to establish as a result of extensive introductions (deliberate and accidental) which have expanded their natural ranges, a consequence of their economic importance.

The Salmoninae have both freshwater and anadromous representatives, while the Thymallinae are restricted to freshwater alone. All Coregoninae except *Coregonus oxyrhyncus* are also freshwater inhabitants.

All Salmonidae breed in freshwater. There are no strictly marine forms, or any that spawn in the sea. This feature has been used to support the hypothesis that they have a freshwater origin (Tchernavin, 1939:18).

Because of their economic significance the reproductive strategies of the Salmonidae have been the centre of much attention and an extensive volume of literature has accumulated on the subject (e.g. Shapovalov & Taft, 1954; Hartman, 1959; Frost & Brown, 1967; Carlander, 1969; and Havey & Warner, 1970). A summary of this information is beyond the scope of this study.

The Salmonidae are generally carnivorous, and feed on a variety of freshwater and marine organisms. Food preferences vary according to size and development of the predator. The juveniles while in freshwater generally feed on insect larvae, but as adults, food items include a variety of fish and Crustacea (Dymond, 1963:482; Bănărescu, 1964). Most salmonids can be considered opportunistic feeders.

In spite of extensive biological and taxonomic literature concerning salmonid fishes, little attention has been given to the interrelationships of the included taxa. Some authors have presented phylogenetic speculations (see below for a full summary). However, these have been based primarily on *ad hoc* assumptions of how the taxa evolved. By means of a cladistic analysis (*sensu* Nelson & Platnick, 1981; and Patterson, 1982), this study set out to establish the intergeneric relationships of the Salmonidae using comparative osteology and myology.

This study also considers the question of outgroup relationships, as the interrelationships of the 'Salmoniformes' are in as much disarray as are the intrarelationships.

TAXONOMIC HISTORY

As discussed above, the intrarelationships of the Salmonidae and indeed the 'Salmoniformes' is the source of much confusion and is still in a state of flux.

Early ichthyologists, not concerned with lower level relationships, grouped together the salmonid taxa with little consideration for their intrarelationships. Early classifications (e.g. Regan, 1913:289) put the Salmonidae into the order Isospondyli, an order first conceived by Cope (1871). However, Berg (1940) believed the Isospondyli to be an unnatural group, and erected the order Clupeiformes to include, among others, the Salmonidae. The order Clupeiformes is a grade, based on a combination of characters (Berg, 1940:417) many of which are now considered plesomorphic for teleosts

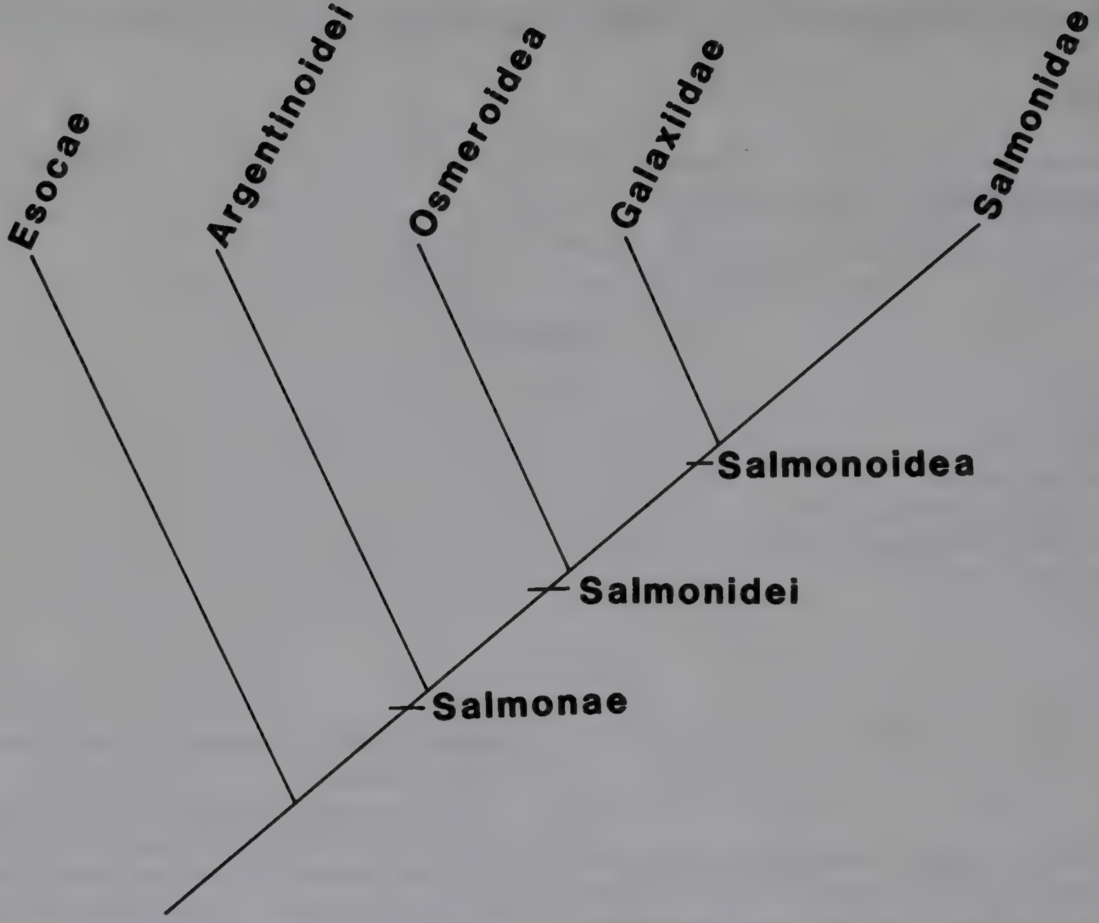

Fig. 1 Classification of salmoniform fishes (after Rosen, 1974).

(e.g. mesocoracoid usually present, scales usually cycloid). Indeed Berg states: 'This order ... represents an artificial assemblage.'

This idea persisted until Greenwood *et al.* (1966) redefined the Clupeiformes and created a division, Protacanthopterygii, which included four orders, one of which was Salmoniformes. This concept of Salmoniformes encompassed many taxa which have subsequently been removed (e.g. Stomiatiformes, Mychtophiformes, and neoscopelids; for a full summary see Lauder & Liem, 1983:132).

Rosen (1973, 1974) was the first author to consider the classification of the Salmoniformes in any detail, and this he did using a cladistic approach. He concluded that the Esocae, Argentinoidei, Osmeroidea, Galaxiidae and Salmonidae comprise the Salmoniformes (Fig. 1).

Fink & Weitzman (1982:85) and Fink (1984:205) considered the Salmoniformes a non-monophyletic group and hypothesized the Salmonidae to be the sister group to the Neoteleostei (Fig. 2).

Bonaparte (1832) originally used the family name Salmonidae, but did not list the included taxa. The three sub-families of the Salmonidae I recognise here: the Salmoninae, Thymallinae, and Coregoninae have been in a constant state of flux. Cope (1871, 1872) considered the Coregoninae a family, using the character of parietal bones meeting in the midline as justification. Gill (1893, 1895) incorrectly stated that the Coregoninae like *Salmo* have parietals that are separated by the supraoccipital, and thus elevated the third group of salmonids, the Thymallinae to family rank. This misobservation was corrected by Boulenger (1895) who stated there was '... no reason for separating *Coregonus* and *Thymallus* from the Salmonidae.'

The Thymallinae has been recognized as a family several times (Jordan & Evermann, 1896; Tchernavin, 1923; and Berg, 1940).

More recently, Norden (1961) has provided a detailed osteological account of the Salmonidae which he recognised as comprising three subfamilies; Salmoninae, Thymallinae and Coregoninae. Both Norden (1961) and Behnke (1965:19) give detailed historical taxonomic accounts of the family.

Kendall & Behnke (1984) used external, larval and chromosome characters culled principally from published information to produce a cladistic analysis of the Salmonidae. From this analysis they recognised the Thymallinae as the sister-group to the Salmonidae and the Coregoninae the sister-group to those two (Fig. 3).

The most recent phylogenetic anaysis of the Salmonidae is by Smith & Stearley (1989) whose paper was published after this text had been accepted for publication. These authors' results preempt to a certain extent those presented here and their cladograms of generic relationships, based on different and fewer morphological characters and on life-history characters supports the hypothesis of relationships set out here.

Materials and methods

Material

Specimens used for this study include those stored in alcohol, dry skeletons and cleared and double-stained specimens. All

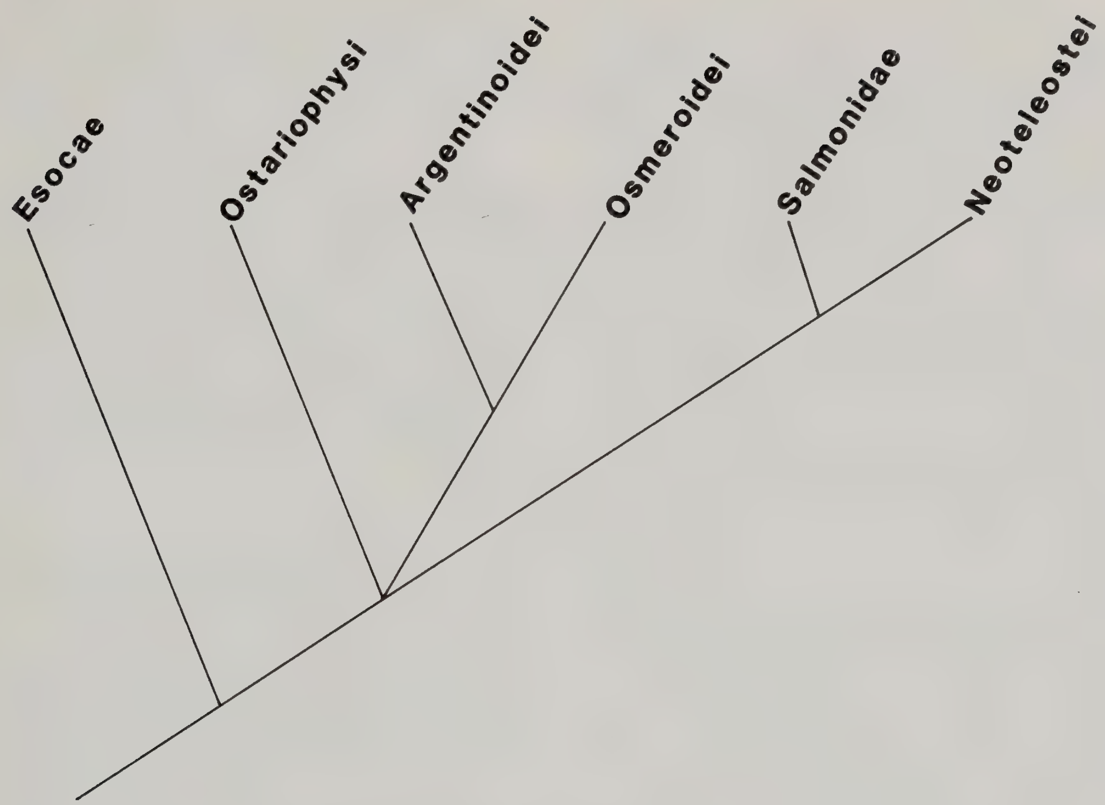
Esocae
Ostariophysi
Argentinoidei
Osmeroidei
Salmonidae
Neoteleostei

Fig. 2 Classification of 'lower' euteleosts (after Fink & Weitzman, 1982).

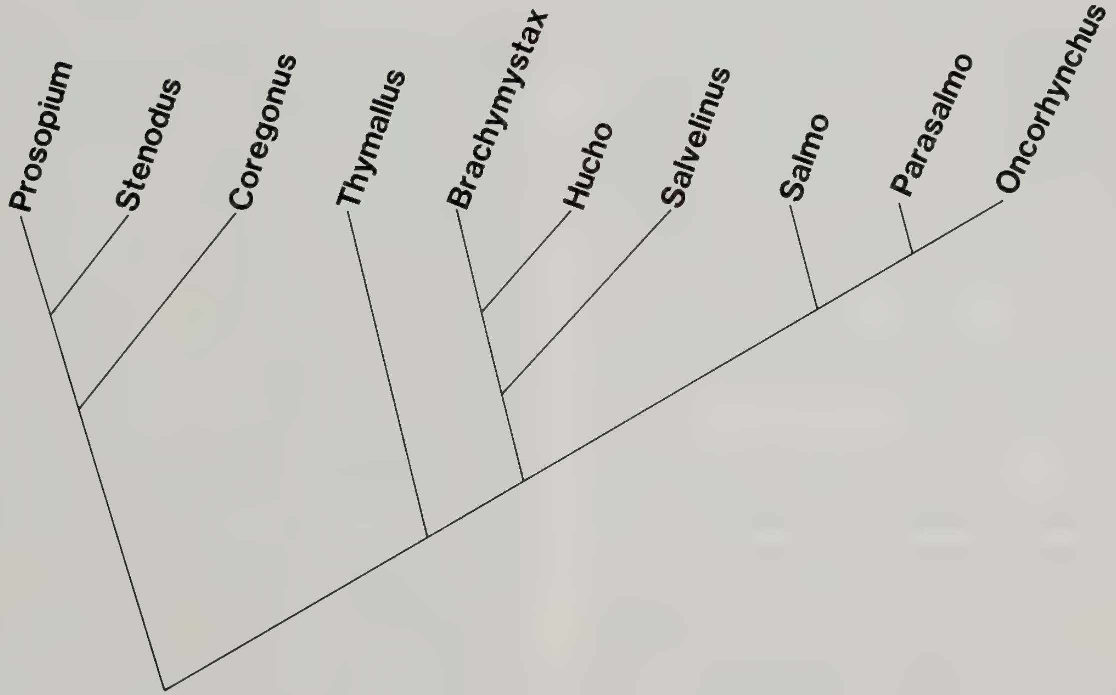
Prosopium
Stenodus
Coregonus
Thymallus
Brachymystax
Hucho
Salvelinus
Salmo
Parasalmo
Oncorhynchus

Fig. 3 Classification of salmonid genera (after Kendall & Behnke, 1984).

material used is held in the BMNH collections. A list of study taxa is give in Table I.

NOMENCLATURAL NOTE. Following recent recommendations of the American Society of Ichthyologists and Herpetologists Committee on Names of Fishes, the specific name of the rainbow trout used here is *mykiss* as distinct from the long-standing *gairdneri* (see Smith & Stearley, 1989 for discussion, and p. 151 below).

Methods

The intra- and interrelationships of the Salmonidae were evaluated using a cladistic analysis (*sensu* Nelson & Platnick, 1981; and Patterson, 1982). To establish those characters (homologies) which define monophyletic groups, knowledge of outgroup conditions is necessary (Patterson, 1982:51). The selection of 'appropriate' outgroups can be highly problematic (e.g. see Maddison *et al.* 1984) and is often based on

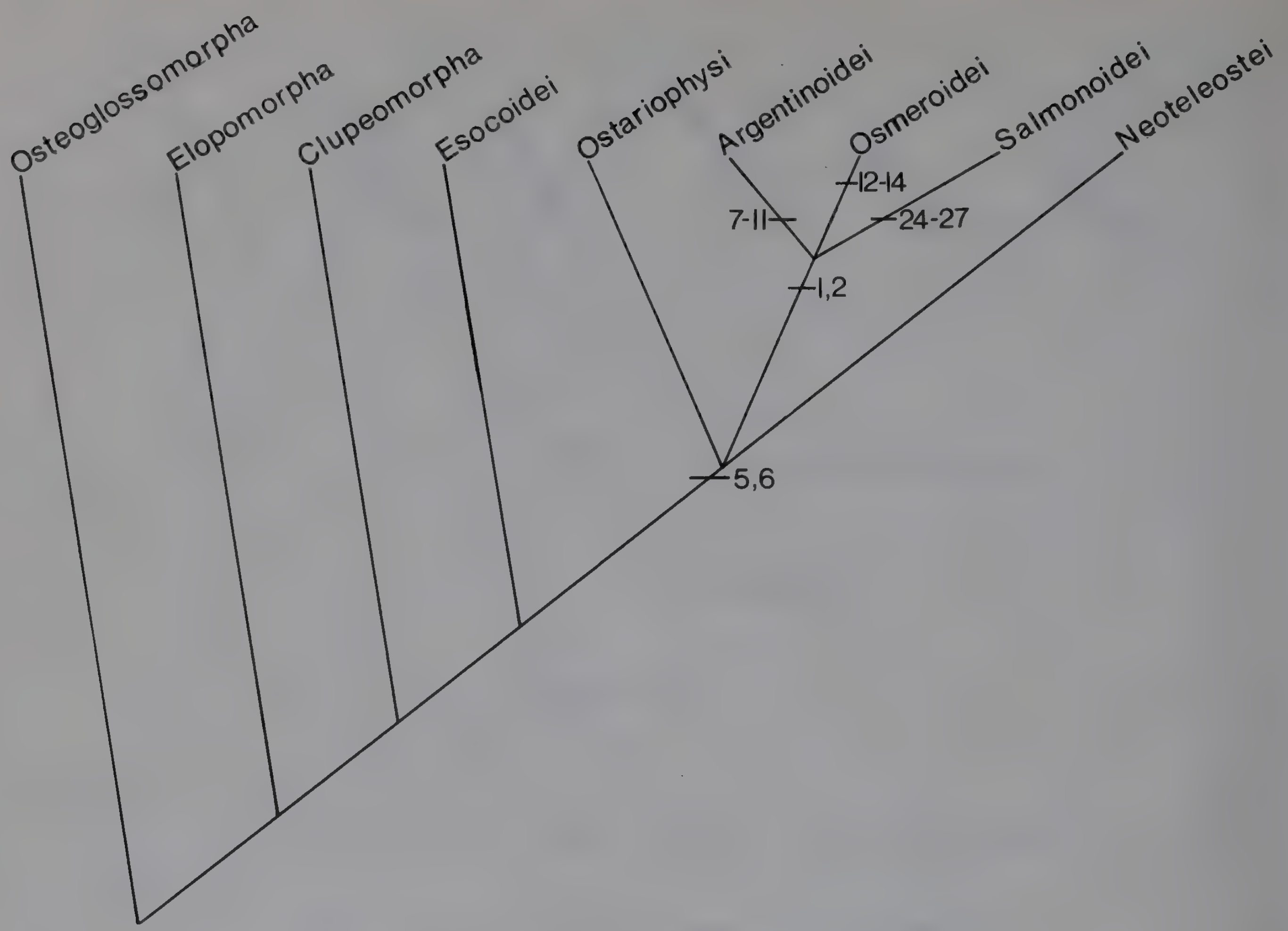

Fig. 4 Cladogram of salmonoid interrelationships. Characters enumerated in the text.

previous hypotheses of interrelationships. It is important to remember that outgroups do not necessarily possess plesiomorphic characters, as the very characters which define the taxon must, by implication, be autapomorphic. Thus, no single taxon can be assumed to be morphologically plesiomorphic for all characters.

In order to reduce the use of homoplastic characters in defining groups, a range of outgroup taxa was used, when possible, to examine the diversity of morphological configurations. As Stiassny (1986:414) points out 'Clearly it is not always the same taxon that bears the plesiomorphous state for each character under consideration.'

Another major criterion for establishing homology or the generality of a character, and thus relationships, is ontogeny (Nelson, 1978; and Patterson, 1982:52). Where possible this principle was employed to support decisions of character polarity, and thus hypotheses of relationships.

For the purposes of this study the Salmonidae (composed of the Salmoninae, Thymallinae and Coregoninae) and its included genera were considered the ingroup. The monophyly of the Salmonidae is based on a tetraploid karyotype (Gold, 1979:389). The first level of outgroup comparison (Unit I outgroup) was based on those taxa which Rosen (1974) included in the 'Salmoniformes'. Rosen's attempts at establishing monophyly of the 'Salmoniformes' have met harsh criticism (Fink & Weitzman, 1982; Lauder & Liem, 1983:132). Consequently, a second level of outgroup comparison (Unit II outgroups) has been used to minimize mistakes when making decisions of character polarity. This second level of comparison was aimed at a wide range of teleost fishes, from so-called 'primitive' groups (e.g. osteoglossomorphs, elopomorphs and clupemorphs) to those which can be considered phylogenetically 'derived' (e.g. Stomiiformes, Paracanthopterygii and Acanthopterygii). For a list of taxa used in Unit I and Unit II outgroups, see Table I.

The dramatic morphological changes which some salmonids undergo when maturing have been well documented (Tchernavin, 1918, 1937, 1938b, and 1943); for example, hyperdevelopment of the ethmoid region, and loss of the teeth at certain developmental stages. While these changes can be important in formulating lower level taxonomic hypotheses; such modifications make comparison with outgroups rather problematic as no outgroup shows such extensive morphological changes. As pointed out by Nijhout *et al.*, (1986:455); 'Examining characters from earlier ontogenetic stages was also useful in that it allowed us to recognize homologous features prior to their concealment by subsequent differentiation.'

A taxonomic study of the Salmonidae requires a comprehensive review of their anatomy. As *Salmo salar* is the type species of the genus *Salmo*, a detailed account of the osteology of this species formed the basis for comparison with other salmonid taxa. The osteological characters utilized were of the ethmovomerine, anterior orbital, otic and occipital regions of the cranium; the jaws, hyopalatine, branchial and hyoid arches; opercular series; pectoral and pelvic girdles; vertebral column; dorsal, anal and caudal fin skeletons.

No complete morphological account of *Salmo salar* has been published and although Norden (1961) included Salmoninae in his osteological account, his descriptive emphasis was on Thymallinae. In contrast, the myology of other salmonids has been the subject of some attention. The cranial and body musculature of *Oncorhynchus tshawytscha* has been described by Greene & Greene (1913), and the cranial myology of *Salvelinus fontinalis* was described by Lauder & Liem (1980). However, the myology of *Salmo salar* has not been discussed but was used in this study as the basis of comparison, first to other salmonids and secondly to outgroups.

In addition to cranial muscles, other characters involving ligaments of the ethmoid region; scales, nasal flaps and papillae, and breeding tubercles were used.

The osteological and myological descriptions with accompanying illustrations and relevant discussions determining character polarity which form the basis of the following hypotheses of interrelationships are not included here. These data are available as microfiche from Natural History Museum Publications.

Interrelationships of the Salmonidae

The results of the character comparisons and analyses have revealed that the Salmonidae is a monophyletic group (see below under 'intrarelationships'). The following hypothesis of interrelationships is summarized in Fig. 4.

The Salmonidae, Argentinoidei (*sensu* Greenwood & Rosen, 1971) and Osmeroidei (*sensu* Fink & Weitzman, 1982) together comprise a monophyletic group synonymous with Rosen's (1974) Salmonae, and are recognized by the following synapomorphies (the numbers preceding each character refer to their position in the cladogram, Fig. 4):

1) Absence of radii on scales
2) Well-developed teeth on the margin of the basihyal (independently derived in osteoglossomorphs, e.g. *Hiodon* and *Notopterus*)

The Salmonidae and Argentinoidei are united by the following synapomorphy:

3) Autogenous neural arches anterior to the dorsal fin. (considered to have been independently derived in some clupeomorphs)

The Osmeroidei and Argentinoidei are also united by an apparent homologous loss:

4) Absence of a maxillary-premaxillary ligament

Fink & Weitzman (1982:84) also suggest that fusion of the posterior neural arches with either the uroneural or first ural centrum is a condition uniting argentinoids and osmeroids but this appears to be of doubtful phylogenetic significance.

The relationships of the Salmonidae, Osmeroidei and Argentinoidei thus remain in doubt, and they are recognized as forming an unresolved trichotomy. Because in this proposed scheme of relationships the Salmonidae of previous authors (e.g. Norden, 1961) is ranked at the same taxonomic level as the suborders Osmeroidei and Argentinoidei, it is elevated to subordinal status, *viz*. Salmonoidei (Fig. 4).

The Salmonoidei, Osmeroidei and Argentinoidei (= Salmonae of Rosen, 1974) are considered to form one of the lineages of a second trichotomy comprising the Neoteleostei and the Ostariophysi. This hypothesis of relationships is based on two synapomorphies:

5) Loss of a toothplate over basibranchial 4 (also Lauder & Liem, 1983:134)
6) Fusion of the first preural and first ural centra

While I also agree with Fink & Weitzman (1982:85) that the Salmonoidei are one of the unresolved sister-groups of the Neoteleostei, I disagree that the two characters they use to propose this hypothesis are synapomorphic at this level. The first of these characters, a *tripartite occipital condyle* is, I believe, a homology of the Salmoninae, and is independently derived in neoteleosts, and some osteoglossomorphs (for discussion, see microfiche).

The second character used by Fink & Weitzman (*loc.cit*) is the presence of *rostral cartilages*. However, rostral cartilages have a more widespread distribution than given by these authors and are thus regarded as characters of little phylogenetic significance.

The following taxa can be defined by suites of autapomorphies, in addition to those used by Greenwood & Rosen (1971), Fink & Weitzman (1982) and Howes & Sanford (1987*a*, 1987*b*).

The Argentinoidei (*sensu* Greenwood & Rosen, 1971) comprising the superfamilies Argentinoidea and Alepocephaloidea:

7) Lateral displacement of the anterior foramen of the trigemino-facialis chamber
8) Fusion of the 1st, 2nd and 3rd supraneurals in Argentinoidea only
9) An extensive *dilatator opercularis* muscle originating in part from the hyomandibular
10) Presence in some alepocephaloids of an A_1 division of the *adductor mandibulae* muscle
11) Absence of a maxillary-ethmoid ligament

Osmeroidei (*sensu* Fink & Weitzman, 1982) comprising the families Osmeridae and Galaxiidae:

12) Two foramina in the *pars jugularis*
13) A deep lamellate second uroneural
14) An open gutter-like preopercular canal

Galaxiidae (= Galaxiinae and Retropinninae). For the relationships of *Lovettia* and *Aplochiton* see Fink (1984):

15) Absence of a third uroneural
16) A low number of branched (principal) caudal fin rays
17) A double palatine-maxillary ligament
18) A double palatine-ethmoid cartilage ligament
19) Absence of a maxillary-ethmoid ligament

Osmeridae:

20) Formation of a semi-tubular ossification arising from the base of the *pars jugularis*

Esocae:
  Esocidae:
    Esox:
      21) Expanded (antero-posteriorly) neural arches of the anterior region
      22) Absence of a palatine-maxillary ligament
    Dallia:
      23) An ossified Baudelot's ligament

Intrarelationships of the Salmonoidei

As discussed under taxonomic history (p. 145) theories of the intrarelationships of the Salmonoidei, like those of their

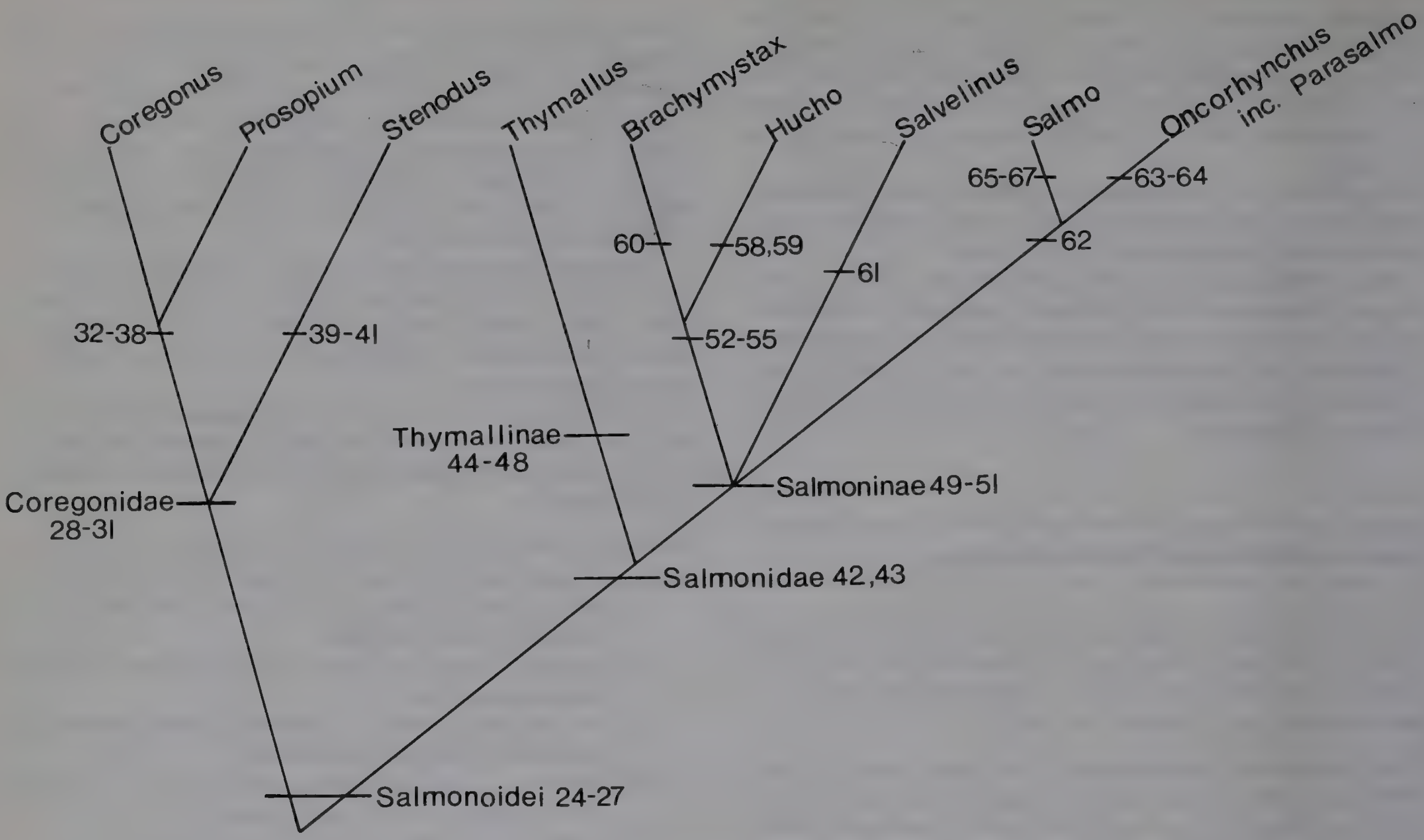

Fig. 5 Cladogram of salmonid intrarelationships. Characters enumerated in the text.

interrelationships, have been in a constant state of flux. This study has, however, revealed that the Salmonoidei (i.e. the Salmonidae *sensu* Norden, 1961; Fink, 1984; and Kendall & Behnke, 1984) are indeed monophyletic. The synapomorphies which define the Salmonoidei are:

24) Tetraploid karyotype
25) A deep posterior myodome, with the eye musculature passing through the myodome and attaching to the trunk muscles
26) A peg-and-socket arrangement of the posterior haemal arch elements of the caudal region
27) An anterodorsal process on the medial pelvic radial element

The suite of characters (homologies) listed below attest to the following hypothesized relationships, which are summarized as a cladogram (Fig. 5).

The Coregonidae (*Coregonus, Prosopium* and *Stenodus*) can be united on the following synapomorphies:

28) The presence of a dorsal flange in the posterodorsal region of the symplectic bone
29) A continuous articulation between the palatine and ethmoid cartilages
30) A short palatine bone
31) Absence of a palatine-premaxillary ligament

In contrast to the views of Kendall & Behnke (1984), who regard *Stenodus* and *Coregonus* as forming a monophyletic lineage with *Prosopium* as its sister-group, I consider *Coregonus* and *Prosopium* as a monophyletic group with *Stenodus* as its sister-group. Monophyly of *Coregonus* and *Prosopium* is supported by:

32) Presence of a separate supra- and rostrodermethmoid
33) Absence of vomerine teeth
34) A well-developed posterior myodome
35) An anteroventral process of the hyomandibular
36) Lack of any association between the palatine and maxilla
37) An expanded ventral region of the posttemporal bone
38) General absence of the ethmoid ligaments, in particular the maxillary-ethmoid ligament

Autapomorphic characters for *Stenodus* are:

39) A second flange on the lateral face of the hyomandibular bone
40) Absence of a medial strut on the mesocoracoid
41) Divison of the A_2 section of the *adductor mandibulae muscle into* A_2a and A_2b

Characters establishing the Salmonidae (Thymallinae and Salmoninae as defined here) as a monophyletic assemblage are:

42) A well-developed 'palatine hook' where the cartilaginous region of the palatine forms a hook over the maxillary head
43) A reduced first proximal pterygiophore of the anal fin

Synapomorphic characters for the Thymallinae are:

44) A concave interface at the posterior symphysis of the pelvic basipterygia
45) Absence of an orbitosphenoid
46) The pattern of the latero-sensory canal in the last infraorbital
47) Papillae in the nasal region, between the nasal flaps

48) A minimum of 17 dorsal fin rays

Synapomorphies for the Salmoninae are:

49) Reduced parietal bones well separated by the supraoccipital
50) A tripartite occipital condyle
51) A suprapreoperculum

Hucho and *Brachymystax* have previously been united as a monophyletic group by Kendall & Behnke (1984), and I agree with this hypothesis on the basis of:

52) A single row of well-developed teeth along the head of the vomer
53) A plate-like flattened medial process of the posttemporal bone
54) A notch on the ventral surface of the medial proximal radial of the pelvic fin
55) Slender infraorbital bones

The genus *Salvelinus* has been united with *Hucho* and *Brachymystax* by Holčik (1982), on the basis of modified lateral line scales. However, examination of the lateral line scale reveals that there are no unusual features which indicate a close phylogenetic relationship between these three taxa. Despite this character negation, there is another possible synapomorphy which could be used to support Holcik's hypothesis:

56) An undivided border of the rostro-dermethmo-supraethmoid

However, there is also a synapomorphy uniting *Salvelinus, Salmo* and *Oncorhyncus*:

57) The absence of a posteroventral process of the orbitosphenoid

In view of this character conflict *Salvelinus* is represented as one lineage of an unresolved trichotomy (Fig. 5).

Autapomorphic characters for *Hucho* are:

58) A reduced posttemporal fenestra
59) A truncate vertical shaft of the hyomandibular bone

Autapomorphic for *Brachymstax* is

60) A second flange in the posterior region of the hyomandibular bone

An autamorphy for *Salvelinus* is:

61) A fragmented lateral extrascapular bone

As there are no autapomorphic characters indicating that *Cristivomer* (Gill & Jordan, 1878) should be regarded as a separate genus, it is here recognized as a synonym of *Salvelinus*. *Oncorhynchus* and *Salmo* are recognized as sister-groups on the basis of their having:

62) A well-developed vomerine shaft bearing well-developed teeth for its entire length

Salmo as presently defined (e.g. Norden, 1961), contains species from both Atlantic and Pacific waters. During the course of this study it has become clear that those *Salmo* species having their original distribution in the rivers of the western coastal region of north America should be included in the genus *Oncorhynchus* (see below).

Synapomorphies which define *Oncorhynchus* are:

63) The intercalar bone extends anteriorly to contact the prootic
64) The exoccipital bone has three foramina (*cf.* two in *Salmo*), the third being for the passage of the occipital nerve

This referral of the Pacific coast *Salmo* to *Oncorhynchus* was also proposed by Regan (1914). The Pacific coast *Salmo* species have also been regarded as constituting a separate subgenus (*Parasalmo* Vladykov, 1963). However, no synapomorphies have been discovered to indicate that the Pacific *Salmo* should be regarded as a group distinct from *Oncorhynchus* (see also Smith & Stearley, 1989).

It is interesting to note that recent analysis using protein electrophoretic techniques (e.g. Ferguson & Fleming, 1983; Berg & Ferris, 1984; and Johnson, 1984) has also indicated that the Pacific coast *Salmo* species are more closely related to *Oncorhynchus* than to the Atlantic coast *Salmo*.

Salmo can be defined on the basis of:

65) A pronounced notch in the anterior region of the ethmoid cartilage, and a well-developed 'kype' in the adult, where the lower jaw curves up and is accommodated by a large pocket in the roof of the mouth
66) An anterior, medially directed process of the metapterygoid
67) A truncate posterodorsal process on the operculum

As there are no autapomorphies indicating that *Salmothymus* (Berg, 1908) should be regarded as a separate genus, it is here recognized as a synonym of *Salmo*.

The above hypothesis of relationships, summarized as a cladogram (fig. 5), is presented in the following revised classificatory scheme:

Suborder Salmonoidei (new usage)
  Family Coregonidae (new usage)
    Subfamily Coregoninae (new usage)
      Genus *Coregonus*
      Genus *Prosopium*
    Subfamily nov. Stenodinae
      Genus Stenodus
  Family Salmonidae (new usage)
    Subfamily Thymallinae
      Genus *Thymallus*
    Subfamily Salmoninae
      Genera *Hucho*
        Brachymystax
        Salvelinus
        Salmo
        Oncorhynchus

Proposed Changes in Taxonomic Ranking

Because, in this proposed scheme of relationships the Coregoninae of previous authors (e.g. Norden, 1961), is ranked at the same taxonomic level as the family Salmonidae, it must be elevated to family status, *viz*. Coregonidae. In addition, the Salmonidae of previous authors (e.g. Norden, 1961; Kendall & Behnke, 1984) is here restricted to include the genera *Thymallus, Hucho, Brachymystax, Salvelinus, Salmo* and *Oncorhynchus*.

Taxonomic conclusions arrived at here support Smith & Stearley's (1989) adoption of the generic name *Oncorhynchus* for the Pacific basin species and *Salmo* for the Atlantic and Eurasian species of salmon.

Listed below are those species assigned to *Oncorhynchus* and *Salmo* (based principally on Behnke, 1965); the validity of some species has yet to be ascertained.

Oncorhynchus: aguabonita Jordan, 1892; *apache* Miller, 1972; *chrysogaster* Needham & Gard, 1964; *clarki* Richardson, 1836; *gilae* Miller, 1950; *mykiss* Walbaum, 1792 (*gairdneri* Richardson is a synonym).

Salmo: *ischchan* Kessler, 1877; *obtusirostris* Heckel, 1852; *ohridanus* Steindachner, 1892; *pallaryi* Pellegrin, 1924; *platycephalus* Behnke, 1968; *salar* Linnaeus, 1758; *trutta* Linnaeus, 1758; *zetensis* Hadzisce, 1960.

ACKNOWLEGEMENTS. I gratefully acknowledge the Trustees of the British Museum (Natural History) for providing me with room and facilities during the period of my doctoral study.

Loans and gifts were generously provided by T. Abe (University of Tokyo), K. Alt (Alaska Department of Fish & Game), R. Carveth (University of British Columbia), E. Crossman (Royal Ontario Museum), M. Himberg (Finland), S. Kullander (Swedish Natural History Museum), D. McAllister (National Museum of Canada), J. Thorpe (FFL, Pitlochry), and S. Weitzman (U.S. National Museum).

I am also grateful to members of the BMNH Fish Section who have always given me valuable assistance, B. Brewster, J. Chambers, O. A. Crimmen, P. H. Greenwood, M. Holloway, A. C. Wheeler and P. J. P. Whitehead. I also thank C. Patterson (BMNH) and W. Fink (University of Michigan) for spending much time on and providing valuable criticisms of the manuscript (micro-fiche version). I also thank G. V. Lauder (University of California) in whose laboratory I was able to work on the editing.

A special word of thanks goes to Andrew Milner (Birkbeck College, University of London) who has always been a caring, understanding and supportive supervisor only too willing to give help. Finally, most heart-felt thanks to Gordon Howes (BMNH) who has always remained a constant source of inspiration and guidance.

The work was primarily funded by NERC grant GTS/84/ALS/1 with additional support from grant GT8/87/ALS/1 and NSF grant DCB 8710210 to G. V. Lauder.

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Table I List of taxa studied arranged in taxonomic categories (see text for explanation of outgroups).

SALMONIDAE: Coregoninae; *Coregonus albula*, *C. lavaretus*, *C. nasus*, *Prosopium cylindricus*, *P. williamsoni*, *Stenodus leucichthys*. Salmoninae; *Brachymystax lenok*, *Hucho hucho*, *H. perryi*, *H. taimen*, *Oncorhynchus clarki*, *O. gorbuscha*, *O. kisutch*, *O. masou*, *O. mykiss*, *O. nerka*, *O. tchawytscha*, *Salmo obtusirostris*, *S. salar*, *S. trutta*, *Salvelinus alpinus*, *S. fontinalis*, *S. malma*, *S. namaycusch*. Thymallinae; *Thymallus arcticus*, *T. brevirostris*, *T. thymallus*.

UNIT I OUTGROUPS: Argentinoidei; *Alepocephalus bairdi*, *A. rostratus*, *Argentina silus*, *A. sphyraena*, *Searsia koefoedi*. Escoidei; *Dallia pectoralis*, *Esox americanus*, *E. niger*, *Umbra krameri*, *U. pygmaea*. Galaxiidae and associated taxa; *Aplochiton zebra*, *Galaxias fasciatus*, *G. fontanus*, *G. maculatus*, *G. platei*, *Paragalaxias dissimilis*, *Prototroctes maraena*, *Retropinna retropinna*, *Stokellia stokellia*. Osmeridae and associated taxa; *Hypomesus olidus*, *Mallôtus villosus*, *Osmerus esperlanus*, *O. mordax*, *Plecoglossus altivelis*.

UNIT II OUTGROUPS: Clupeomorpha; *Clupea harengus*, *Ethmalosa dorsalis*, *Etrumeus teres*, *Odaxothrissa lasera*, *Sardinella aurita*, *Sprattus sprattus* Elopomorpha; *Albula vulpes*, *Elops* sp., *E. hawaiensis*, *E. machnata*, *Megalops cyprinoides*. Neoteleostei; *Dicentrarchus labrax*, *Gadus morhua*, *Lepomis macrochirus*, *Maurolicus mulleri*, *Merluccius merluccius*, *Normanichthys crockeri*, *Pollichthys mauli*, *Saurida gracilis*, *Synodus foetens*. Ostariophysi; *Alestes dentex*, *Chanos chanos*, Osteoglossomorpha; *Hiodon alosoides*, *Osteoglossum bicirrhosum*, *Scleropages formosus*, *S. leichhardti*.

Bull. Br. Mus. nat. Hist (Zool.) **56**(2): 155–203 Issued 25 October, 1990

A Review of the Bathygadidae (Teleostei: Gadiformes)

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SYNOPSIS. The taxonomic status and relationships of the gadiform genera *Bathygadus* Günther, 1878 and *Gadomus* Regan, 1903 are reviewed in the light of characters shared with macrouroids and gadoids. The genera are recognised as sister-taxa which constitute the family Bathygadidae. Relationships of the family are ambiguous since it exhibits only gadiform symplesiomorphies, and might therefore represent the sister-lineage to all gadiforms.

The osteology and soft anatomical features of *Bathygadus* are described. The taxonomy of *Bathygadus* and *Gadomus* is reviewed; 10 species of the former and 12 of the latter are recognised. Bathygadid distribution is centred above the Equator in both Atlantic and Indo-Pacific oceans; no bathygadids are recorded from the eastern Pacific.

INTRODUCTION

The taxonomic status and relationships of 'bathygadines'

Traditionally, *Bathygadus* and *Gadomus* have constituted the subfamily Bathygadinae of the family Macrouridae. Regan (1903) gave as characters for the Bathygadinae:

> First vertebra articulating with the skull, its neural spine not directly attached to the occipital crest. First dorsal ray not spinous. First gill-arch entirely free anteriorly.

Regan also included in the Bathygadinae the genera *Melanonus*, *Lyconus* and *Trachyrincus*. Subsequent removal of these taxa (see below) left only *Bathygadus* and *Gadomus* in the subfamily. The revised diagnosis of that group (Okamura, 1970*a*; Marshall & Cohen, 1973) relies on characters plesiomorphic for Gadiformes (and for 'paracanthopterygians') ie. mouth wide, terminal; rows of small or minute jaw teeth; premaxillae with relatively short pedicels, slightly protractile; seven branchiostegal rays; olfactory bulbs close to the forebrain; first gill-arch unrestricted; gill-rakers on 1st arch long and numerous; abdominal vertebrae 11–13; pelvic fin with 8 or 9 rays; scales without spinules; swimbladder with 2 or 4 retia, no drumming muscles; no light organs (Marshall & Cohen, 1973). Nasal bones small, separated; lachrymal without medial ventral bony plate; symplectic slender; hyomandibular without lateral ridge; ethmoid not enlarged into plate dorsally; interosseus spaces between symplectic and preoperculum and between preoperculum and operculum (Okamura, 1970*a*).

If these characters are plesiomorphic among gadiforms what are the derived characters which define 'bathygadines' and what justification is there for considering *Bathygadus* and *Gadomus* as macrouroids or gadoids? To consider these questions the diagnostic features of those two groups are examined.

MACROUROIDEI

Regan (1903) listed characters for the Macrouridae and Gadidae, concluding that 'The Macruridae (*sic*) . . . in the two essential characters of the more posterior ventrals and absent caudal, are less specialized than the Gadidae . . .' Other macrouroid characters listed by Regan are, apart from 'vertebrae numerous' not confined to that group but nevertheless form the bases of subsequent diagnoses by Okamura (1970*a*, *b*) and Marshall & Cohen (1973). Regan's concept of the Macrouroidei included *Bathygadus* and *Gadomus* and other genera (*Lyconus*, *Macruronus* and *Steindachneria*) which Marshall (1966) included in the Gadoidei. Marshall (1966) also detailed certain characters as gadoid and others as macrouroid (see below). Okamura (1970*a*, *b*) followed Regan's diagnosis of macrouroids, incorporating features identified by Marshall (1966) and others of his own, concluding (1970*a*) that the absence of a caudal fin is '. . . the only constant characters by which the macrouroids can be separated from other gadiforms.' Marshall & Cohen (1973) also utilized Regan's character of the 1st vertebra not being closely joined to the skull and recognised as specializations: absence of caudal fin and presence of broad lateralis canals, light organ, and spine-like element in the 1st dorsal fin. All authors cited agree on the absence of a caudal fin (as a correlate, the caudal skeleton) as diagnostic for macrouroids. However, the gadoid *Steindachneria* also lacks a caudal fin and skeleton, and the 'macrouroid' *Trachyrincus* has a modified fin and skeleton (Howes, 1989). Okamura (1970*a*, *b*), Marshall (1973*a*) and Marshall & Cohen (1973) list

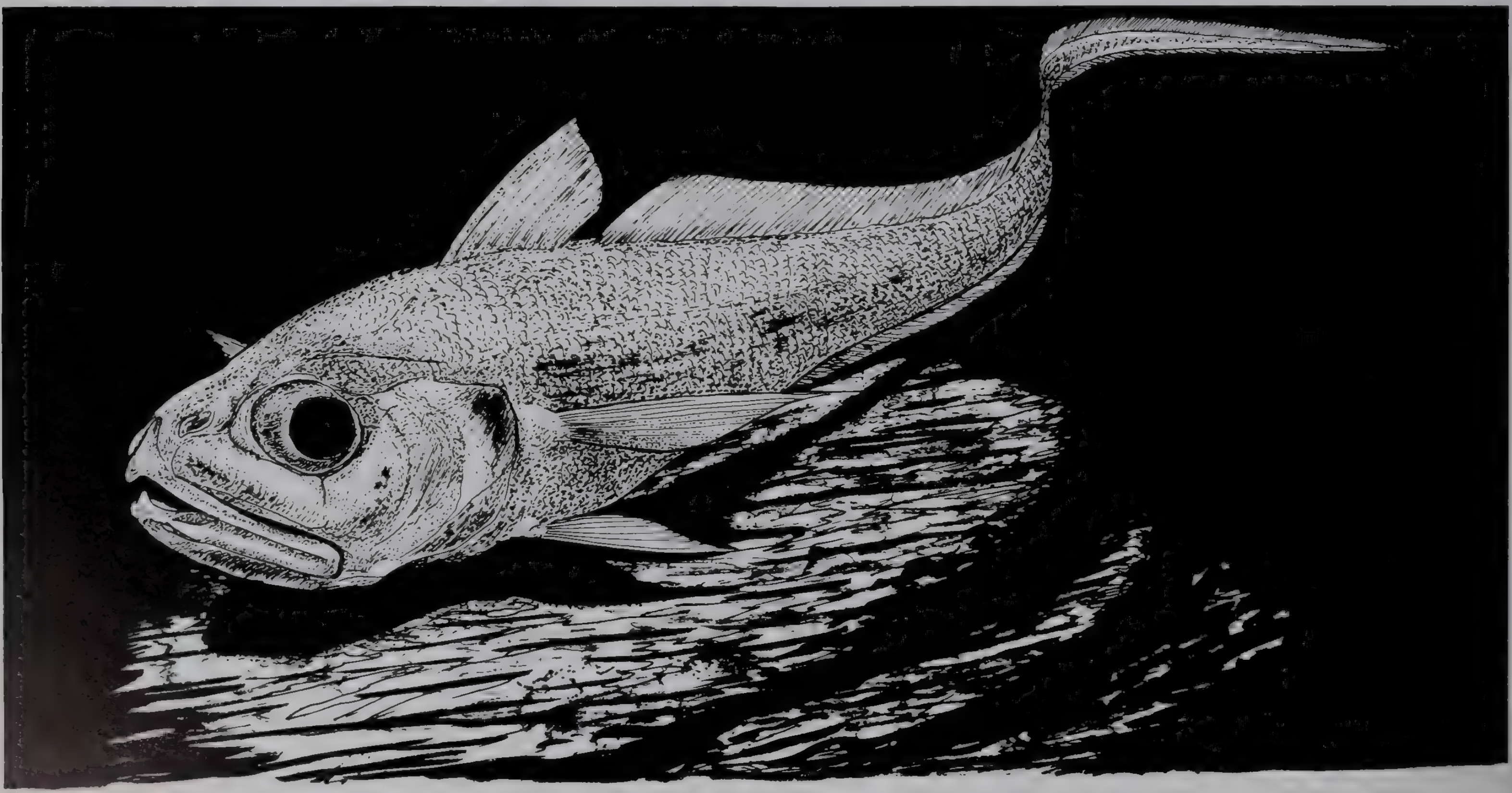

Fig. 1 A bathygadid in assumed swimming mode. Reconstruction based on photograph taken by remote controlled camera (Pl.2) in Marshall & Bourne, 1964); drawn from a specimen of *Bathygadus melanobranchus ca* 280mm TL.

characters apparently synapomorphic for macrouroids if one excludes *Bathygadus* and *Gadomus*; these characters are as follows:

Scales keeled or spinigerous

Okamura (1970*a*, *b*) recognised that *Bathygadus* and *Gadomus* differed from other macrouroids in possessing cycloid scales with a reticulate pattern on the exposed surface. The scales of macrouroids (including *Trachyrincus*) are often keeled and bear spiniferous processes on their exposed area.

Infraorbitals

Okamura (1970*b*:38) noted that the lachrymal of macrouroids is divided by a ventral longitudinal plate, absent in *Bathygadus*, *Gadomus* and gadoids.

Palatine bone

Okamura (1970*b*:46) recognised different palatine morphotypes between *Bathygadus*, *Gadomus* and macrouroids, being deep with a shallow lateral depression in the former and shallow with a medial lateral ridge in the latter. Howes (1988) noted that macrouroids have a loose ligamentous connection between the palatine and ventral and lateral surfaces of the lateral ethmoid. Unlike *Bathygadus* and *Gadomus* and gadoids there is no contact with the ethmovomerine bloc or mesethmoidal part of the lateral ethmoid.

Expansion of the symplectic

The symplectic is deep and posteriorly expanded to contact the leading edge of the preoperculum (Okamura, 1970*b*).

Upper jaw accommodation

Okamura (1970*b*:55) noted in macrouroids 'With the exception of *Gadomus* and *Bathygadus*, a large space or cavity, into or out of which the premaxillary pedicel slides, is formed between the nasal and ethmoid'. This 'cavity' results from an anteriorly truncated ethmoid bloc and a medially and anteriorly extended nasal and is a character complex unique to macrouroids.

Nasals joined in midline

Okamura (1970*b*:55) and Marshall (1973*a*:498) recognised that expanded nasals, joined in the midline and bearing a median crest are diagnostic for macrouroids. The nasals in *Bathygadus* and *Gadomus* although large and cavernous remain medially separated or in contact only posteriorly.

Ethmoid produced into a high vertical plate

Okamura (1970*a*, *b*) noted that the ethmoid forms a vertical plate with a posterior extension in macrouroid taxa other than *Bathygadus* and *Gadomus* (see also p. 162).

Macrouroid subfamilies

Characters recognised by Regan (1903) and subsequent authors as diagnostic for the subfamily Macrourinae, *viz*: 1st gill-slit restricted by membraneous fold; short, denticulate gill-rakers on 1st arch; drumming muscles connected to swimbladder and light organs are synapomorphic as are ligaments connecting the nasal bone to the maxilla and the attachment of the maxillary-premaxillary ligament to the rostral cartilage (Howes, 1989). The subfamily Macrouroidinae is characterized by cranial and other anatomical specializations (see Okamura, 1970*a*, *b*; Marshall, 1973*a*; Howes, 1989).

GADOIDEI

Gadoids have been defined ambiguously by the presence of a homocercal caudal fin skeleton. Regan's (1903) Gadidae, corresponding to most later authors' Gadoidei, differed from the macrouroids '. . . only in the more anterior ventrals, which have 1–9 rays, and in having a separate caudal fin'. Reliance on the derived absence of the caudal fin in macrouroids leaves gadoids characterized by symplesiomorphies.

Svetovidov (1948) noted an osseus canal formed from ventral laminae of the frontal which provides a channel for the olfactory tracts in gadoids. Usually, the tracts lie adjacent to one another, but in macrouroids they are separated for much of their length by the interorbital septum.

Rosen & Patterson (1969) recognised a 'gadoid caudal skeleton', being homocercal and having a particular fusion pattern of hypurals, involving procurrent rays and often the presence of superior and inferior elements (termed X and Y bones).

Howes (1989) recognised the Gadoidei by a ligament connecting the interoperculum to the preoperculum and hyomandibular; reduction (including loss) of *obliqui ventrales* muscles on the laterally compressed 1st and 2nd gill-arches, and indirect attachment (*via* the *rectus communis* muscle) of the *sternohyoideus* muscle to the urohyal.

Markle (1989) outlines a concept of the Gadoidei based on loss of an interarcual cartilage, position of the scapular-coracoid foramen, high number of pre-caudal vertebrae and two separate hypural plates. Patterson & Rosen (1989) consider the first two of these characters as synapomorphies for the Gadiformes but they do not remark on the monophyly of the Gadoidei.

Characters shared by *Bathygadus* and *Gadomus* with macrouroids

Specialized characters shared by *Bathygadus*, *Gadomus* and macrouroids are:

1. Two spinous rays in the 1st dorsal fin (Okamura, 1970*a*, *b*; Marshall, 1973*a*)
2. Supraoccipital crest separated from 1st neural spine (Regan, 1903; Marshall, 1973*a*).

Spinous dorsal rays have a restricted disjunct distribution among gadiforms. In the Macrouroidei, the two genera *Macrouroides* and *Squalogadus* in the subfamily Macrouroidinae lack the feature. In the Gadoidei, Moridae and Merlucciidae possess a single spine (reduced in the former and in *Macruronus* of the latter). In Okamura's (1970*b*) opinion, not backed by evidence, spinous rays were not remnants of a former primitive condition but a neomorph. This question may be resolved by observing, in those taxa lacking dorsal spines, their presence during ontogeny.

Separation of the supraoccipital crest from the 1st neural spine is a plesiomorphic feature; a high crest separated from the spine is present in the Lower Eocene gadoid *Rhinocephalus* (Rosen & Patterson, 1969:431) and is widespread among 'paracanthopterygians' and acanthopterygians. In *Gadomus*, however, homology of the supraoccipital crest is doubtful since the supraoccipital bone is 'overlain' by a separate element which forms the crest (Figs 7, 8). The overlapping margin of the crest covers the medial border of the exoccipital and the crest may represent the 1st neural spine. The possibility that the 'exoccipital' condyles represent that bone or are the fused facets of the 1st neural spine has been discussed by Rosen & Patterson (1969), Patterson (1975) and Rosen (1985).

There are no identified synapomorphies which relate *Bathygadus* and *Gadomus* to macrouroids. Okamura (1970*b*) listed 25 osteological and 3 soft anatomical differences between 'bathygadines' and macrouroid taxa (Table 1). Only differences pertinent to questions of homology are included in the anatomical descriptions of this text.

Table 1 Contrasting characters in Bathygadidae and Macrouroidei. Compiled from data given in Okamura (1970*b*).

Character	Bathygadidae	Macrouroidei
1 Scales	reticulate	spiniferous
2 Outer gill-arch	unrestricted	restricted by fold of skin
3 Outer gill-rakers	slender	short and spinous
4 Premaxillary teeth	villiform	larger; various
5 Maxilla	slender with posterior notch	deep, notched
6 Premaxilla postmaxillary process	ventrally situated	posteriorly situated
7 Retroarticular	J-shaped	L-shaped
8 Mouth	terminal, protrusibility limited	inferior, protrusile
9 Lachrimal with ventral lamina	absent	present
10 Palatine	deep	shallow
11 Quadrate-preopercular space	present	absent
12 Symplectic	expanded dorso-posteriorly	expanded ventro-posteriorly
13 Hyomandibula	flat	with ventral flange
14 Preopercular width	more than 3 in its length	less than 3
15 Preopercular-symplectic space	present	absent
16 Operculum-preoperculum	separated	operculum overlaps preoperculum
17 Interoperculum, sickle-shaped	in *Bathygadus*	variously shaped
18 Nasal-premaxillary cavity	absent	present
19 Nasals	separated	meet
20 Ethmoid lamina	low	high
21 Frontal	unelaborated	many ridges
22 Hypohyal	oblong	rounded
23 Cleithrum	narrow	broad
24 Rib	on last abdominal vertebra	lacking on last or penultimate vertebra
25 Anal pterygiophores	normal	anteriorly placed, arc-like
26 Swimbladder	thin-walled, few retia	thick-walled, many retia
27 Intestine	simple, S-shaped	elaborate coiling
28 Luminous organs	absent	present in some genera

Characters shared by *Bathygadus* and *Gadomus* with gadoids

Most character states listed in Table I for *Bathygadus* and *Gadomus* are shared with gadoids but these correspondences are mainly plesiomorphic; of the three features Howes (1989) considered synapomorphic, two are found in other gadiforms. The ligamentous attachment of the interoperculum with hyomandibular occurs in some 'ophidiiforms' (see above) and indirect connection of *sternohyoideus* muscle with urohyal occurs in some macrouroids (Howes, 1988). The other character, reduction of *obliqui ventrales* muscles is unique to some Gadoidei.

In summary, there are no features that suggest a close relationship with either macrouroids or gadoids. Gadoids are ambiguously diagnosed (see above). Howes (1990) recognises upper and lower fused hypural plates as diagnostic for a subgroup of 'higher' gadoids, but 'lower' gadoids, including Bathygadidae, Steindachneriidae and Moridae remain a paraphyletic assemblage. The Bathygadidae conform to Stiassny's (1986) dictum of a 'morphologically and phylogenetically primitive lineage' and may eventually be regarded as the plesiomorphic lineage to other gadiforms.

Integrity of Bathygadidae

Howes (1988; 1989) united *Bathygadus* and *Gadomus* on a single synapomorphy (occasional absence of *obliqui ventrales* muscles on 1st gill-arch); other synapomorphies support this relationship and justify recognition of a monophyletic lineage, these are;

1. Development of anterior body muscles where *infracacarinalis anterior* markedly tendinous and well-separated from *hypaxialis* (p. 181);
2. Modified nerve pathway serving pectoral fin rays (p. 182);
3. Reduced gill-filaments (p. 181).

One character shared by *Bathygadus* and *Gadomus* (recognised by Gilbert & Hubbs, 1916 as diagnostic for the Bathygadinae) is that the 2nd dorsal fin rays are longer than those of the anal fin. This feature is not restricted to bathygadids, however, but occurs in *Trachyrincus* (included by Gilbert & Hubbs, 1916 in Bathygadinae). In *Steindachneria* (a 'gadoid'; Fahay, 1989) only the first 10–12 anal rays are lengthened, the remainder reduced; in *Macruronus* (Merlucciidae) and Euclichthyidae anterior anal rays are lengthened; in Moridae, 2nd dorsal has longer rays than anal in *Antimora*, *Physiculus*, *Auchenoceros*, *Mora* and *Tripterophycis*. The feature is not therefore diagnostic for Bathygadidae.

As noted above, it is impossible at present to determine the sister-group of Bathygadidae, but there seems little justification for letting it remain as a macrouroid sub-group (see above). Iwamoto (1989) prefers to recognise 'Bathygadinae' as the plesiomorphic sister-lineage to macrouroids, but he identifies no synapomorphy that unites them with macrouroids. Iwamoto's (1989) reference to Howes' (1989) inclusion of *Gadomus* in Melanonidae was based on a statement in an early draft of that paper and one subsequently revised as published.

METHODS AND MATERIALS

Osteological study was based primarily on cleared and alcian-alizarin stained preparations of *Bathygadus melanobranchus* and *B. macrops* with observations on *Gadomus longifilis* and dry skeletal preparations of these taxa and *Bathygadus favosus*, *B. furvescens* and *Gadomus arcuatus*.

Parameters used are fewer than those of previous authors as most were of little utility. Gilbert & Hubbs (1920) give meristics and counts of up to 27 parameters and features, but the preserved state of their material limits the accuracy of their measurements to at least ± 2mm. Use of total length measurement is discarded as the posterior part of the tail is often broken off and the 'caudal' is merely a regeneration (see p. 179). As the 1st anal fin ray nearly always lies below the 13th vertebra the distance from the snout to this point has been taken as the principal dividend for proportional measurements (**s-a**).

Body depth (**bd**), expressed as % of s-a distance is an unreliable measurement and of limited use as a species-specific character. Head length (**hl**), expressed as % of s-a distance and interorbital width (**io**), expressed as % of head length, are useful indications of specific differences as this part of the fish is little affected by preservation and usually undamaged. Orbital diameter (**od**), expressed as % of head length is taken horizontally from the inner edge of the lateral ethmoid to the inner rim of the posterior infraorbital.

Premaxillary length (**pml**), expressed as % of head length, is measured from the anterior surface of the bone to its distal tip. The length (or height) of the premaxillary ascending process (**pma**), expressed as % of premaxillary length, is measured along its symphyseal margin. The distance across the midline between the premaxillary dentigerous surfaces (**pms**) is expressed as % of premaxillary length.

Dorsal and anal fin rays are often broken and measurements of their lengths are of little value and as the tail is often missing, counts have been limited to the first dorsal fin (**D**) and denote the first two spinous rays thus: II. Pectoral fin length (**pl**) expressed as % of s-a distance; as the outer (usually, prolonged) ray is often broken. Barbel length (**bl**) is given as % of head length. It is unreliable as a specific character (Gilbert & Hubbs, 1920).

Scale counts are not given; Gilbert & Hubbs (1916; 1920) used numbers in transverse rows but differences of two or three scales in these series can occur intraspecifically. Gill-rakers (**GR**) are counted on the 1st arch as those on the epibranchial + those on the ceratobranchial (the raker sometimes overlapping the elements is counted with those on the ceratobranchial). Pyloric caeca (**PC**) have been counted where possible.

Specimens examined for anatomy

Material is listed in alphabetical order of genera and species. D=dissected; A=cleared and stained; S=dry skeleton.

GADIFORMES: *Antimora rostrata* 1986.4.22:10–11(A); *Bathygadus favosus* 1963.2.25:26–27 (S); 28–30 (D); *B. furvescens* 1939.5.24:670–672 (D); *B. macrops* 1973.3.5:3–6 (A); *B. melanobranchus* 1969.6.26:3227–31 (A, D); 1963.2.3:31–35 (D); 1934.12.19:26–27(A, tail only); *Bregmaceros atripinnis* 1889.2.1:3988–91 (D); *Brosme brosme* (two skulls uncat.); *Coelorinchus caribbaeus* 1963.2.25:244–250 (A); *C. coelorinchus* 1905.2.2:18(S); *Euclichthys polynemus* 1986.5.14:1–3(D); *Gadomus arcuatus* Uncat. (A, tail only); *G. longifilis* 1963.2.25:7–17(D); 1890.6.16:43(S); 1965.2.25:7–17 (S, A); *Gadus morhua* 1971.2.16:628–633(A); *Gaidropsarus mediterraneus* uncat.(A); uncat.(S); *Halargyreus johnsonii* 1981.3.16:406–7(D); 1973.10.29:384–440(D, A); 1968.5.13:1(A); *Lepidion eques* 1981.3.16:437–44(A); 1902.10.30:4(S); *Lota lota* 168.6(S, two skulls); 1953.6.26:15–18(D); *Lotella marginata* 1976.9.28:6–7(A); *Macruronus magellanicus* 1936.8.26:342–51(D); *M. novaezelandicus* Uncat.(S); *Malacocephalus laevis* 104.11.30:33(S); *Melanonus zugmayeri* 1981.3.16:377(D); *Merluccius merluccius* 1971.7.21:44–57 (D; A); *M. productus* 1896.9.25:6(S); *Merlangius aeglefinis* Uncat.(S); *Microgadus proximus* 1984.12.5:45–48(D); *Molva molva* Uncat. (S, skull); *Mora moro* Uncat. (S); *Muraenolepis microps* 1937.7.13:24–29(D; S); 1937.7.12:11–17(A); *Nezumia aequalis* 1973.3.5:60–4(A); *Phycis blennoides* 1972.2.22:73–6(D); 1898.4.30:14 (S); Uncat. (14 skulls); *Physiculus marginatus* 1936.8.26:424–431(A); *Raniceps raninus* 1967.1.1:4(D); 1893.7.6:2(A); 1884.8.26:3(S); *Salilota australis* 1936.8.26:394–404(A); *Steindachneria argentea* 1963.2.25:325–9(D); 344–54(A); *Trachonurus villosus* 1963.2.25:226–8(D); *Trachyrincus trachyrincus* 1976.7.30:42–53 (D, A); 1888.6.15:7(S); *Trisopterus luscus* Uncat. (S, 8 skulls); *Urophycis regia* 1985.6.6:109–119(A); *Ventrifossa occidentalis* 1965.2.25:61–71(D, A).

OPHIDIIFORMES: *Acanthonus armatus* 1887.12.7:55, 56 (syntypes); *Bassosetus compressiceps* 1887.13.7:47–8(D); *Brotula jayakari* 1891.2.9:30(S); *Carapus bermudensis* 1985.6.6:138–83(A); *Cataetyx messieri* 1936.8.26:1060–1(D); *Dicrolene introniger* 1939.5.24:1441–4(D); *Echiodon drummondi* 1967.5.4:3–5(D); *Genypterus blacodes* 1896.6.17:73(S); *Glyptophidium macropus* 1986.10.6:49–50(D); *Hypopleura caninum* 1986.10.6:63–5(D); *Lamprogrammus exutus* Uncat. Discovery Colln.; *L. fragilis* 1939.5.24:1493–96(D); *L. nigricans* 1939.5.26:1483–7(D); *Monomitopus metriostoma* 1964.8.6:47–54; *Neobythites steaticus* 1910.1.31:11(S); *Ophidion rochei* 1971.12.17:6–8(D); *Sirembo armatus* 1938.6.23:27–8(D); *Thalassobathia pelagica* 1967.11.8:1(D);

OTHER TAXA: Gadopsiidae *Gadopsis marmoratus* 1914.8.20:228–233(A); Liparidae *Careproctus longipinnis* 1956.5.1:6–8(D).

Institutional abbreviations

Material examined for the anatomical study is from the collections of the Natural History Museum, London (BMNH); specimens used in the taxonomic review are also from BMNH and from the J. L. B. Smith Institute of Ichthyology, Rhodes University (RUSI), the United States National Museum of Natural History (USNM) and the Zoologisch Museum of Amsterdam University (ZMA).

Abbreviations used in the figures

Bones and ligaments

aa	anguloarticular
aap	articular process of premaxilla
ac	actinost
ahy	anterohyal
ap	ascending process of premaxilla
apr	articular process of radial
ar	anal fin ray
ard	anal fin radial
asc	'accessory' supraoccipital crest
bb	basibranchial
bh	basihyal
bo	basioccipital

bof	basioccipital facet
br	branchiostegal ray
cac	caudal cartilage
cb	ceratobranchial
cl	cleithrum
cm	coronomeckelian bone
co	coracoid
cr	caudal ray
d	dentary
dar	distal dorsal radial
dh	dorsohyal
dr1 & 2	dorsal fin rays of 1st and 2nd dorsal fins
drd	dorsal fin radial
ds1 & 2	dorsal fin spines
eb	epibranchial
ect	ectopterygoid
els	enlarged lateral line scale
ent	entopterygoid
ep	epioccipital
epr	epipleural rib
ex	exoccipital
f	frontal
fh	foramen for hypobranchial nerve
fm	foramen magnum
fmc	medial frontal crest
fmlc	medio-lateral frontal crest
fIX	foramen for glossopharyngeal nerve
fX	foramen for vagus nerve
hop	opercular process of the hyomandibular bone
hs	haemal spine
hy	hyomandibular bone
hyf	hyomandibular fossa
hyh	hypobranchial
iac	interarcual cartilage
ic	intercalar
ih	interhyal
io	infraorbital (numbered)
iop	interoperculum
ios	interorbital septum
lb	Baudelot's ligament
le	lateral ethmoid
lfc	lateral frontal crest
lpp	lateral process of the pelvic bone
mc	mesocoracoid
me	mesethmoid
met	metapterygoid
ms	membraneous stay
msc	mandibular sensory canal
nas	nasal bone
ns	neural spine
nsf	neural spine articular facet
op	operculum
pa	parietal
pac	parietal crest
pal	palatine
pb	pelvic bone
pbb	pharyngobranchial (numbered)
pc	postcleithrum
phy	posterohyal
pmp	postmaxillary process of the premaxilla
po	preoperculum
pp	parapophysis of centrum
ppe	pelvic process
pr	pleural rib
pro	prootic
ps	parasphenoid
ptc	pterotic crest
pte	pterotic
ptp	posttemporal process of the intercalar
pts	pterosphenoid
ptt	posttemporal
q	quadrate
ra	retroarticular
rc	rostral cartilage
re	rostrodermosupraethmoid
sc	scapula
scl	supracleithrum
so	supraoccipital
soc	supraoccipital crest
sop	suboperculum
sp	sphenotic
spc	scapular articular process of the cleithrum
sy	symplectic
tp	pharyngobranchial tooth-plate
v	vomer
vh	ventrohyal

Soft anatomical features

abs	*abductor superficialis* muscle
abp	*abductor profundus pelvicus* muscle
ad	*arrector dorsalis* muscle
adp	*adductor profundus* muscle
ads	*adductor superficialis* muscle
apv	*arrector dorsalis pelvicus* muscle
asp	*abductor superficialis pelvicus* muscle
av	*arrector ventralis* muscle
avc	anterior vertical canal
avp	*arrector ventralis pelvicus* muscle
cc	cerebellar corpus
dex	dorsal segment of *epaxialis* muscle
ge	granular eminence
hc	horizontal canal
hs	horizontal septum
hx	*hypaxialis* muscle
ica	*infracarinalis anterior* muscle
ls	*lateralis superficialis* muscle
mo	medulla oblongata
ms	medial septum
na	acoustic nerve
ne	neuromast
nll	lateral line nerve
nI, II, V, VII, IX, X	the cranial nerves
pps	pelvic-cleithral tendinous sheet
oll	olfactory lobe
opl	optic lobe
pvc	posterior vertical canal
RLA	*ramus lateralis accessorius* nerve
—A	anal branch
—D	dorsal branch
—P	pectoral branch
—PP	pectoral-pelvic trunk
sa	sacculus
sca	*supracarinalis anterior* muscle
sh	*sternohyoideus* muscle
vex	ventral segments of *epaxialis* muscle

ANATOMY OF *BATHYGADUS*

Osteology

In dorsal view cranium is broadly triangular; in *B. melanobranchus* pterotic region 80% of cranial length; steep dorsal profile and orbital depth of 30% of its length. Crania of *Gadomus* species narrower than *Bathygadus* (see diagnoses). High supraoccipital crest, depth of occipital part of cranium exceeding length. Skull bones of both *Bathygadus* and *Gadomus* papery, fragile and lateral borders of cranial roofing bones irregular.

Olfactory region (Figs 2 & 3)

Ethmoid bloc: Dorsal profile cruciform, dorsal surface and posterior lamina fully ossified; unity with underlying ethmoid cartilage suggests it is a *rostrodermosupraethmoid* (*sensu* Patterson, 1975); ossified portion and underlying part of ethmoid cartilage is a compressed plate. Ethmoid cartilage slopes forward anteriorly and expands laterally and is trowel-shaped (Fig. 2A, re & me). *Lateral ethmoid* (le, Figs 2B, 3) contacts ethmoid cartilage ventromedially; thin lamellate lateral wing; dorsomedial lamina of bone contacts frontal. *Vomer* (v, Fig. 2) short, narrowly triangular with thick, convex anterior border; extends level with lateral ethmoid posteriorly; ventral surface deeply concave and edentulous (Fig. 2C).

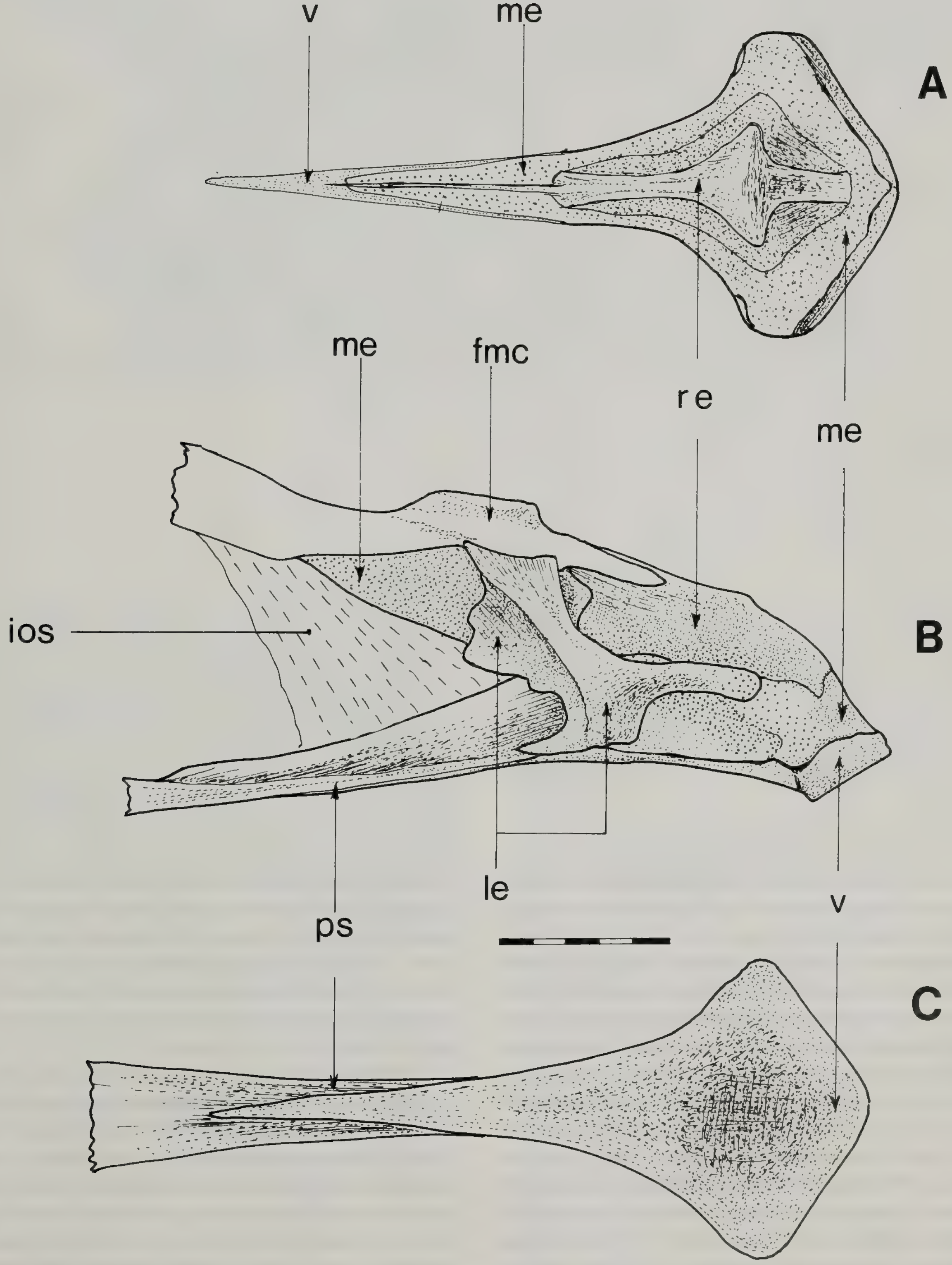

Fig. 2 *Bathygadus favosus* (BMNH 1963.2.25:26–7 and following figures). Ethmovomerine region in A, dorsal; B, lateral, and C, ventral views. In A. the parasphenoid and frontals have been removed to show the dorsal surface of the vomer.

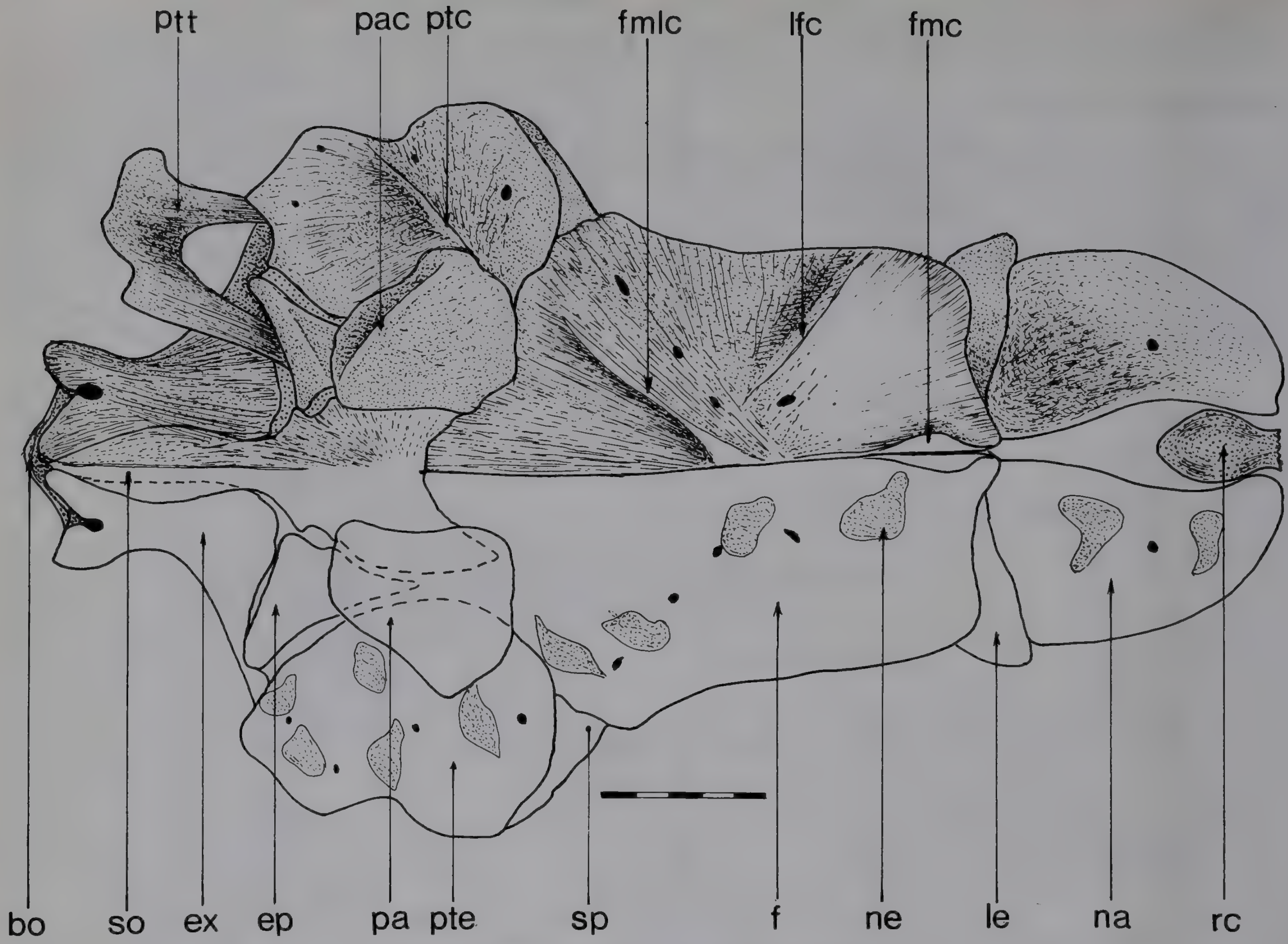

Fig. 3 *Bathygadus favosus*. Dorsal view of cranium.

Nasals large, trough-like, bluntly triangular separated anteriorly by rostral cartilage and ascending premaxillary processes; posteriorly joined in midline by strong connective tissue. Posterior border covers lateral ethmoid, overlapped medially by frontal (Fig. 3). Contains two neuromasts, roofed by skin. In *Gadomus* nasals narrower, broadly separated for their entire length (Okamura, 1970*b*).

COMMENTS. In other gadoids ethmoid region similar to *Bathygadus* being compressed, ossified plate capping flared, medially elevated cartilaginous base. Ethmoid ossification is taxonomically variable; in Moridae, Merlucciidae, Bregmacerotidae and Muraenolepididae, ossified part of ethmoid separated from vomer by narrower area of cartilage than in other groups. Slope of ethmoid variable; in *Melanonus* (Melanonidae) and *Merluccius* (Merlucciidae) ossified part of ethmoid acutely sloped and confluent with anterior surface of ethmoid cartilage but in *Macruronus* and *Lyconus*, also referred to Merlucciidae, ethmoid is gently sloped as in Bathygadidae. In Gadidae, Lotidae, Muraenolepididae and Ranicipitidae, ethmoid profile almost vertical; concave in Bregmacerotidae. Macrouroid ethmoid morphology similar to that of Gadidae etc, except that ossified portion of ethmoid cartilage is thin vertical lamina bearing anterior and posterior extensions (Okamura, 1970*b*:59; fig. 35) a feature synapomorphic for macrouroids (see p. 157). *Trachyrincus* has compressed ethmoid but lacks laminar extensions.

Okamura (1970*b*, fig. 20) incorrectly identified in *Bathygadus* the mesethmoid cartilage as the rostral cartilage.

Among gadoids edentulous vomers occur in Bathygadidae, Euclichthyidae and Muraenolepididae and throughout macrouroids, including *Trachyrincus*. Vomerine teeth variously developed in other gadoids; in Steindachneriidae and Melanonidae single row of small recurved teeth and patch of lateral teeth respectively, outer row teeth in *Melanonus* firmly fixed but larger inner teeth depressible. Vomerine teeth occur biserially in Merlucciidae; in Gadidae, Ranicipitidae and Phycidae teeth more numerous in bands or patches on either side of vomerine head. In Bregmacerotidae, teeth in single row of 3 or 4 along edge of vomerine head, which has prominent anterior extension (D'Ancona & Cavinato, 1965; fig. 18). Patches of vomerine teeth in some genera of Moridae (eg. *Mora*).

Lateral ethmoid in Bathygadidae has single, ventromedial contact point with ethmoid cartilage, as in Melanonidae, but in Steindachneriidae and most other gadoids lateral ethmoid wing contacts parasphenoid medially. Mujib (1967:1361) notes that in *Merluccius* and *Lota* lateral ethmoid has '... the anterior and dorsal processes; the ventral process, which is very prominent in *Gadus*, is entirely lacking'. This is not so, although in Merlucciidae (*Merluccius*) and Lotidae lateral ethmoid extends further posteriorly, greater area of contact with parasphenoid, and more horizontal lateral wing but

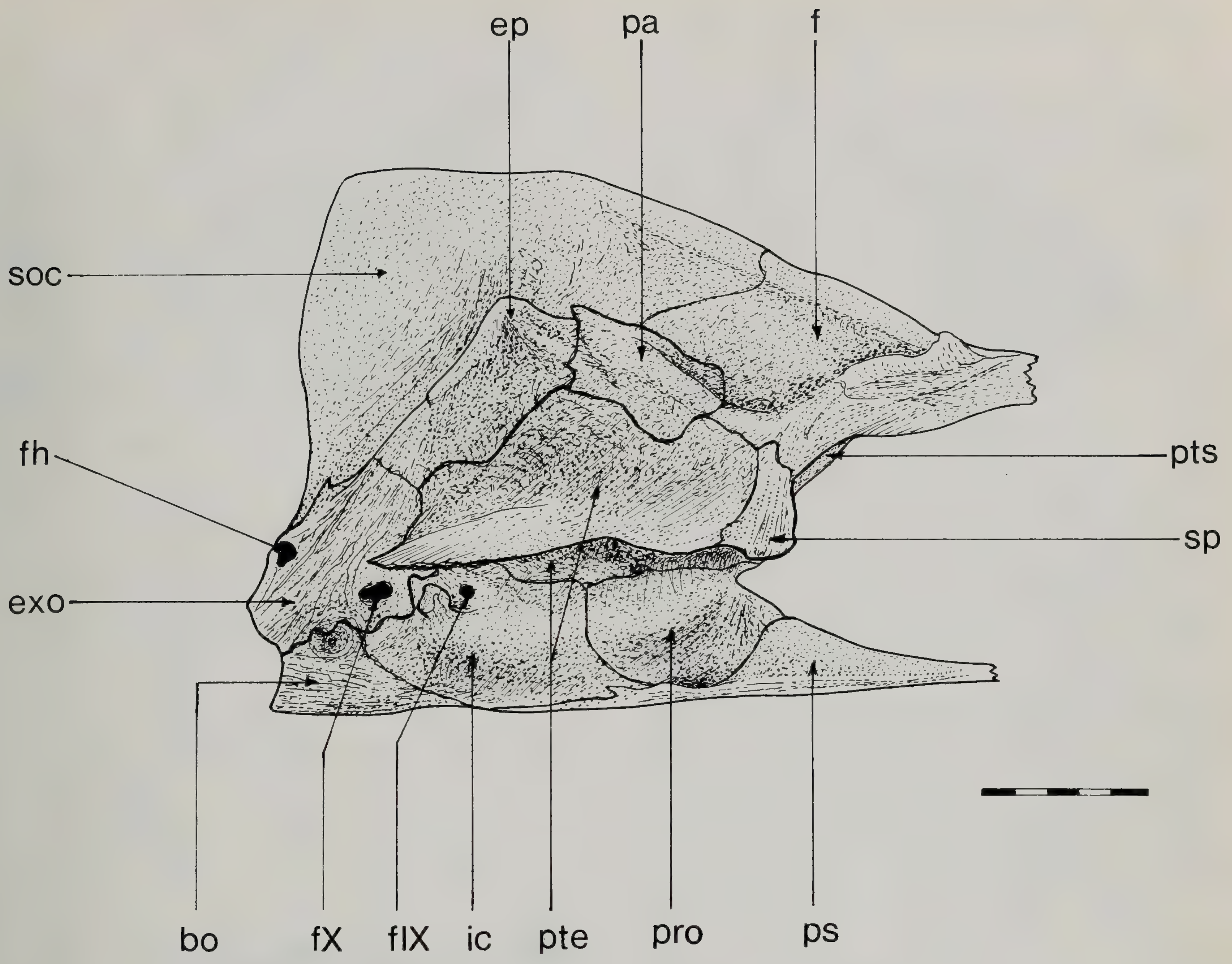

Fig. 4 *Bathygadus favosus*. Lateral view of occipital and otic cranial regions.

retain ventral curvature of wing (called 'ventral process' by Mujib *op. cit.*).

Orbital region (Figs 4, 5)

Pterosphenoids widely separated by optic foramen, each narrowly triangular, lamellate plate overlapping sphenotic posteriorly and contacting medial border of prootic; dorsally, contact with descending lamina of frontal. Anterior border of pterosphenoid contributes to optic fenestra (Fig. 5).

Parasphenoid with flat underside, grooved anteriorly for reception of vomer; dorsally lateral ridges rise anteriorly to meet ethmoid cartilage. Posteriorly shallow ascending process overlaps lower part of prootic; deep ventral indentation between parasphenoid and prootic. At junction of prootic and intercalar parasphenoid widens and overlapped by anteroventral edge of intercalar; narrows posteriorly, forks and sutures to basioccipital; no parasphenoid foramina.

Frontal (f, Fig. 3) broad with slightly concave lateral border above orbit; slight anteromedial crest with right-angled dorsal surface. Diagonal crest extends from lateral point of contact with parietal to midline at centre of frontal. 'Supraorbital' crest anteriorly runs from lateral border of frontal toward centre. Four foramina in each frontal from which exit branches of supraorbital nerve supplying respective neuromasts. Thin lamina extends from ventral surfaces of each frontal in orbital region.

Interorbital septum (ios, Fig. 2B) extends from posterior lamina of ethmoid cartilage to form medial wall to orbital cavity. Septum of thick membraneous tissue extends from lamina of each frontal bone, joining above parasphenoid and forming enclosed channel for olfactory tract. Septum joins prootic, sphenotic and pterosphenoid posteriorly, enclosing rear of orbital cavity. Posterior eye muscles originate from thickened part of septum in midline, anterior to where septum is perforated by optic nerve (Fig. 22C). Where prootic border indented, septal membrane parts from bone leaving opening for trochlear, trigeminal and facial nerve trunks and internal carotid artery.

COMMENTS. Small, widely separated pterosphenoids are commonly encountered in gadoids. Exceptionally, Moridae and some Merlucciidae (*Merluccius*) possess large pterosphenoids forming anterior border to a common trigeminal and facial nerve foramen.

In frontal morphology, bathygadids are plesiomorphic, *viz*.

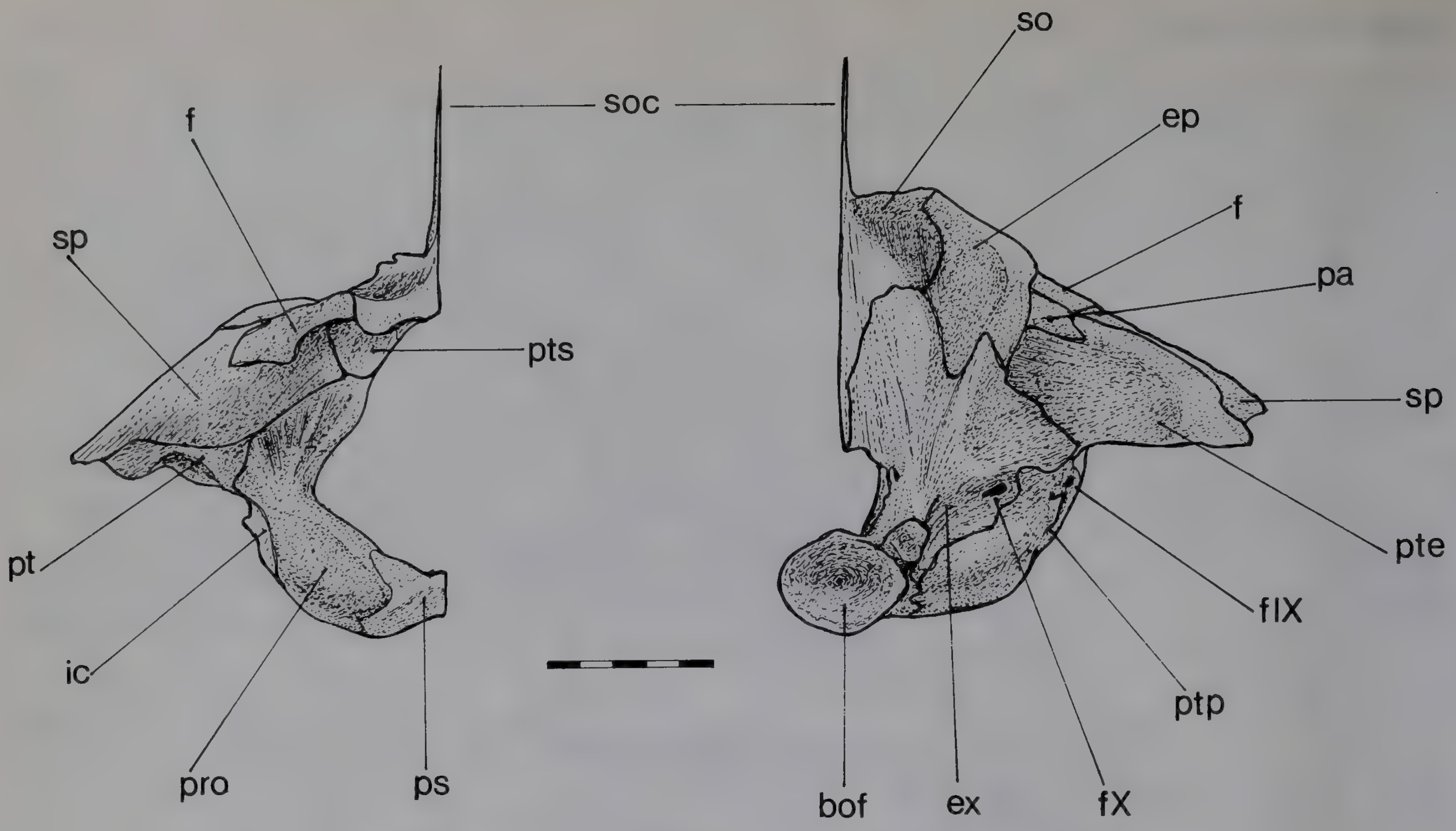

Fig. 5 *Bathygadus favosus*. Cranium in A, anterior, and B, posterior views.

bones broad, bearing simple, X-shaped pattern of ridges and lacking high lateral crest; mucosal cavity absent or wide and open anteriorly. Frontals in gadoids are diverse; in some Gadidae they are narrow interorbitally, fused medially into single plate and have a high lateral ridge; in others mucosal cavity is closed anteriorly (Svetovidov, 1948 illustrations). In Merlucciidae (*Merluccius*) frontal crests in V-formation; in some Phycidae lateral crest uninterrupted and dorsal surface of frontal flat. Development of ventral lamina enclosing olfactory tracts highly variable; lamina may be deep and narrowly separated (*Merluccius*), shallow and narrowly separated (*Molva*, *Phycis*, *Trisopterus*), shallow and broadly separated (*Lota*, *Raniceps*), or deep and narrowly separated anteriorly but shallow and broadly separated posteriorly (*Gaidropsarus*). In Moridae olfactory tracts totally enclosed in osseus canal and interorbital septum usually completely ossified (Svetovidov, 1948; Paulin, 1983), conditions accepted as synapomorphic for the family. Anterior frontal crest variously developed and in some Gadidae (eg. *Trisopterus*) forms medial wall to frontal sensory canal.

Occipital region (Figs 4–6)

The single, median *supraoccipital* is almost square, overlain anteriorly by frontals and laterally by parietals; synchondrally contacts posteriorly epioccipital and laterally pterotic. Supraoccipital crest long and high with a near vertical posterior border. Thin wedge of supraoccipital ventroposterior border forms upper margin of foramen magnum (*cf. Gadomus* where most of foramen's dorsal rim formed by 'supraoccipital' (p. 158; Figs 7, 8). Posteriorly crest narrowly separated from 1st neural spine, a plesiomorphic feature for gadiforms (p. 157).

Posterior cranial wall formed by large *exoccipital* which contacts anterodorsally, supraoccipital and epioccipital *via* synchondral joints, anterolaterally sutured to pterotic and ventrally to intercalar and basioccipital. Posteromedially

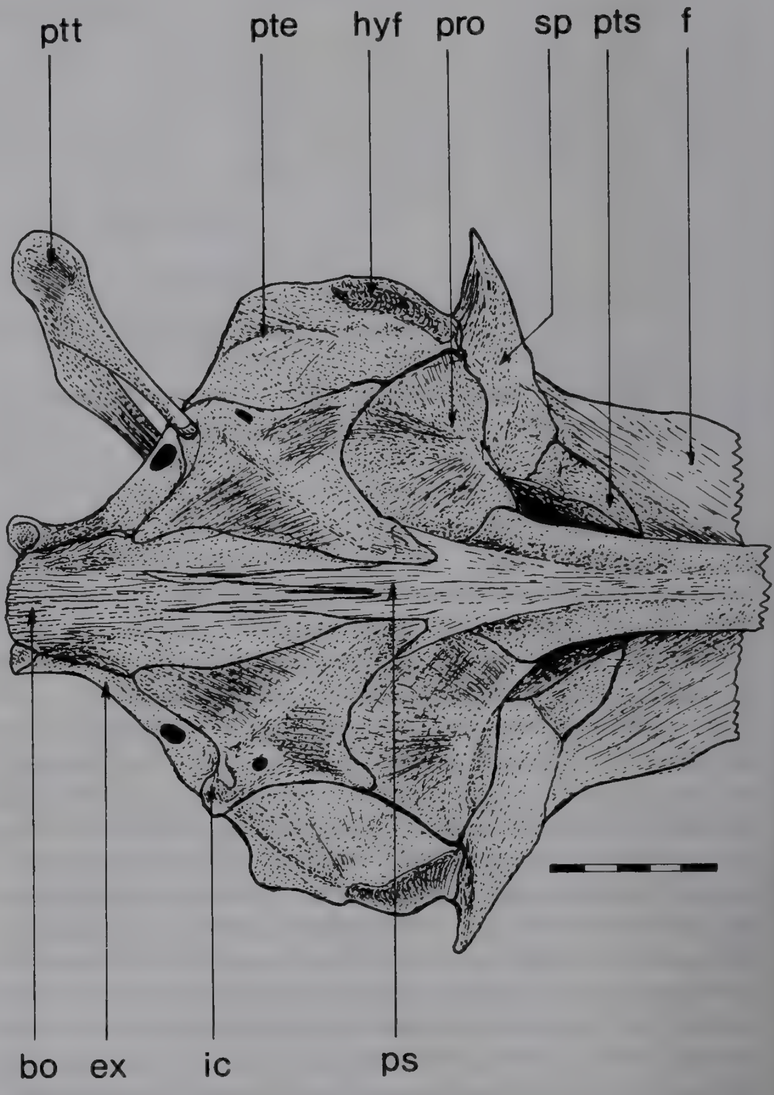

Fig. 6 *Bathygadus favosus*. Basicranium.

exoccipital contributes to border of foramen magnum and posteriorly extends a process whose distal surface forms a fossa for articulation with prezygapophysis of 1st vertebra. Foramen for vagus (X) nerve pierces exoccipital anterolaterally, that for accessory and hypobranchial nerves, posterodorsally.

Basioccipital; single, median bone flooring posterior part of neurocranium (Fig. 6); ventral surface overlain for half its length by parasphenoid; laterally contacts exoccipitals and intercalars; occipital condyle oblate.

Epioccipital; small, pyramidal bone capping posterodorsal corner of cranium, anterodorsal surface overlapped by parietal, medially bordered by supraoccipital, posteroventrally by exoccipital and laterally by pterotic; dorsal surface forms lamboidal crest, contacted by upper limb of posttemporal.

Paired *parietals* small, covering union between pterotic, supraoccipital and epioccipital bones; shallow diagonal crest runs close to parietal posterior border.

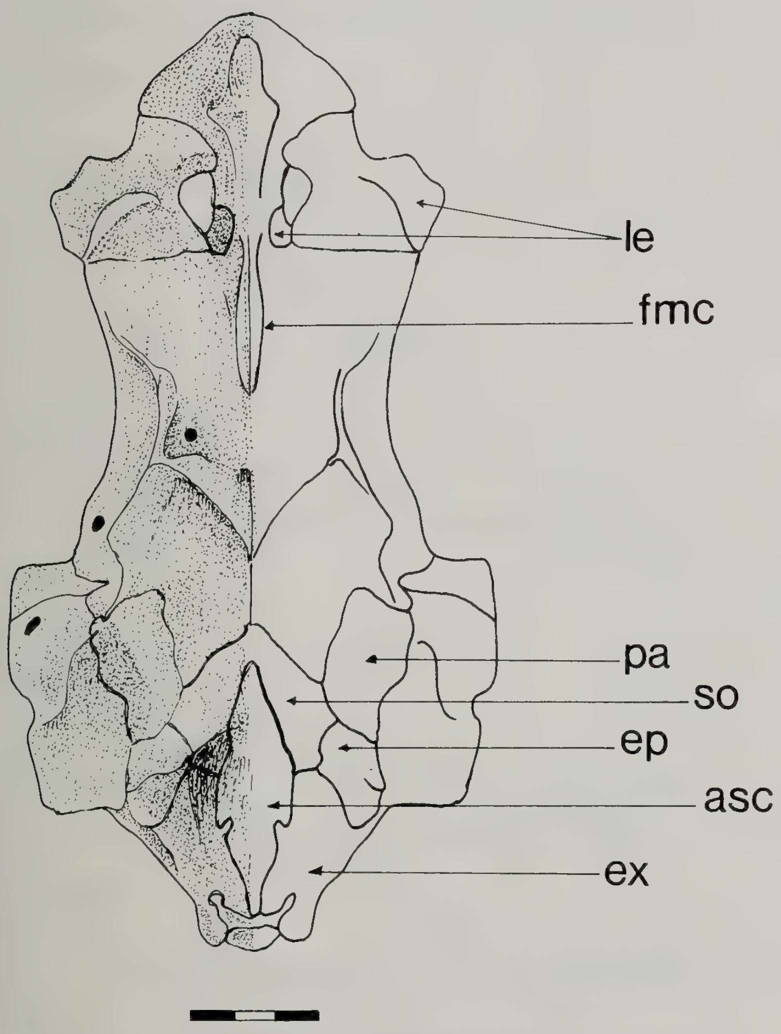

Fig. 7 *Gadomus longifilis* (BMNH 1963.2.25:7–17). Cranium in dorsal view.

Otic region (Fig. 4)

Sphenotic, triangular in dorsal view, overlapped medially by frontal and posteriorly by pterotic leaving narrow area exposed dorsally; anterior, vertical surface lamellar, contacting, anterodorsally, pterosphenoid and ventrally, dorsal rim of prootic.

Pterotic extensive, flaring laterally and roofing nearly entire occipital region; concave dorsal surface receives fan-shaped segment of *epaxialis* muscle (p. 181). Anteriorly, pterotic overlies sphenotic, medially meets both supraoccipital and epioccipital synchondrally, and anteromedially overlain by parietal; ventral margin contacts both intercalar and prootic and posteriorly, exoccipital; ventrally indented by hyomandibular articulatory fossa.

Posterior region of otic bulla formed by *intercalar* which overlaps posteroventral part of pterotic dorsally and anteriorly, posterior third of prootic; ventrally contacts basioccipital and posteriorly exoccipital. Posterolateral face of intercalar bears small protruberance to which attaches lower limb of posttemporal; anterior to protruberance lies glossopharyngeal (IX) nerve foramen.

Prootic forms border of optic fenestra; anterodorsally contacts pterosphenoid and sphenotic, anteroventrally overlapped by ascending wing of parasphenoid; ventral contact with parasphenoid marked by deep unperforated cavity. Posteriorly, prootic overlapped by intercalar and dorsally by pterotic.

Otolith and inner ear. Saccular otolith (Fig. 22) rather elongate with undulating dorsal border; ventral border rounded and smooth; rostrum pointed, posterior margin broadly rounded. Outer surface bears central prominence with two or three indentations close to dorsal border; inner surface smooth, apart from small ostial and caudal colliculi. Otolith nearly spans entire longitudinal opening between saccular and brain cavities. Horizontal canal runs laterally, then posteriorly along wall of prootic-pterotic junction, passing medially to intercalar wall and upward to posterior vertical canal; latter rises into posterior recess of epioccipital; anterior canal lies beneath parietal and pterotic, and runs along mesiad wall of prootic.

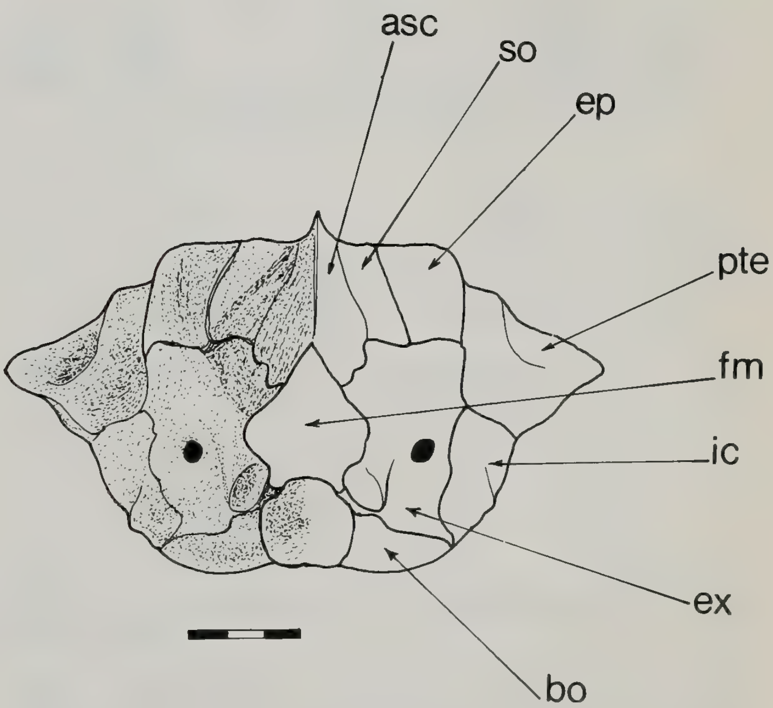

Fig. 8 *Gadomus longifilis* (BMNH 1963.2.25:7–17). Cranium in posterior view.

Circumorbital series (Fig. 9)

First infraorbital (lachrymal) extends from tip of premaxilla to posterior border of eye; sensory canal roofed by outward convexity of bone, lower part of canal covered by skin. Strong, anteriorly situated dorsal process connects infraorbital with ventral surface of lateral ethmoid wing. Contains

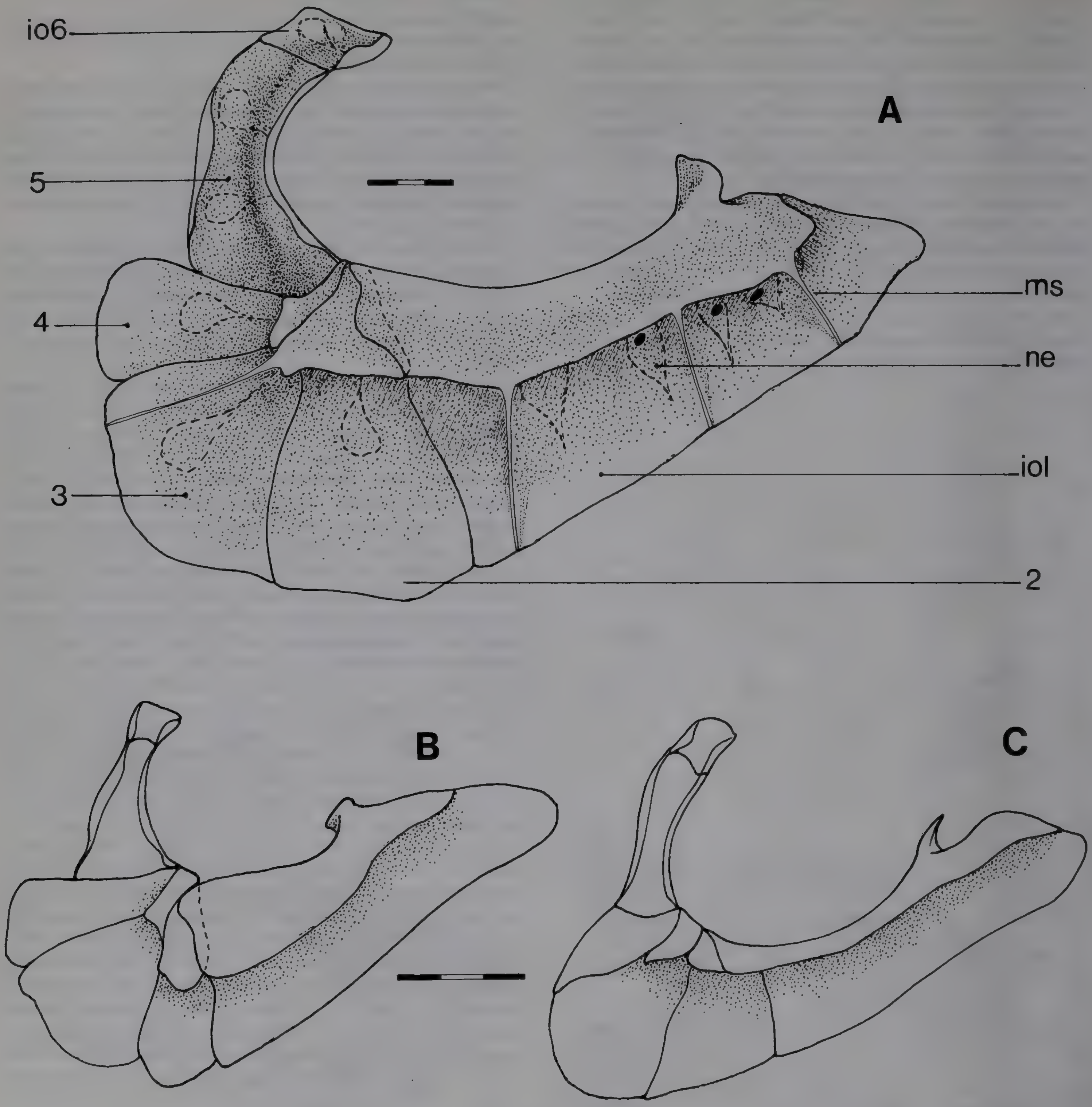

Fig. 9 Circumorbital bones of A, *Bathygadus melanobranchus* (1969.6.26:3227); B. *B. cottoides* (syntype, BMNH 1887.12.7:140.3; C, *Gadomus longifilis* (BMNH 1963.2.25:7–17).

5 neuromasts, two anterior ones close together. *Second infraorbital* as deep as first but only third of its length; orbital border short, bone expanding ventrally. This and subsequent infraorbitals with single neuromast. *Third infraorbital* triangular, forming posteroventral corner of orbit; small portion of bone contributes to orbital rim and marginally forms roof to sensory canal, greater part of canal being covered by skin. *Fourth infraorbital* same length as third, but fifth and sixth half as deep, sixth (dermosphenotic) reduced in length. No antorbital or supraorbital bones.

COMMENTS. Okamura (1970*b*, fig. 21b) shows a marked forward inclination of infraorbitals five and six in *Bathygadus antrodes*; this was not found in any *Bathygadus* examined and it is assumed that Okamura's observation is the result of infraorbital displacement in his specimen. Okamura (1970*b*:38) noted presence in macrouroids of a ventral plate dividing first infraorbital longitudinally; this plate is absent in Bathygadidae and other gadoids but slightly developed in *Trachyrincus*.

Jaw bones (Figs 10, 11)

Maxillaries with strong medial curvature, forming near perfect arc. Each bone thin, narrow and edentulous with slight posterodorsal process at central point of medial curvature (to which attaches muscle A1B); head of bone comprises raised transverse process which contacts ascending process of premaxilla, and an anteriorly directed medial process whose tip is notched to receive ligament connecting with premaxilla (Figs 10A, B). *Premaxillaries* broadly curved toward symphysis; each with tall mid-lateral process bifurcated ascending process and broadly triangular mid-lateral process (postmaxillary process of Rosen & Patterson, 1969; Fig. 10B). Ventral symphysial border of anterior ascending process deeply indented, dentigerous surfaces of two bones widely separated across midline; base of ascending process with deep fossa. Ventral surface toothed, teeth closely and irregularly arranged giving granular appearance to dentigerous surface; teeth unicuspid with flat, inwardly curved tips. Along posterodorsal margin of dentigerous area occur more regularly arranged rows (3 or 4) of smaller teeth, their tips pointing upward.

Rostral cartilage wedge-shaped, held firmly in midline between premaxillary ascending processes (Fig. 10A).

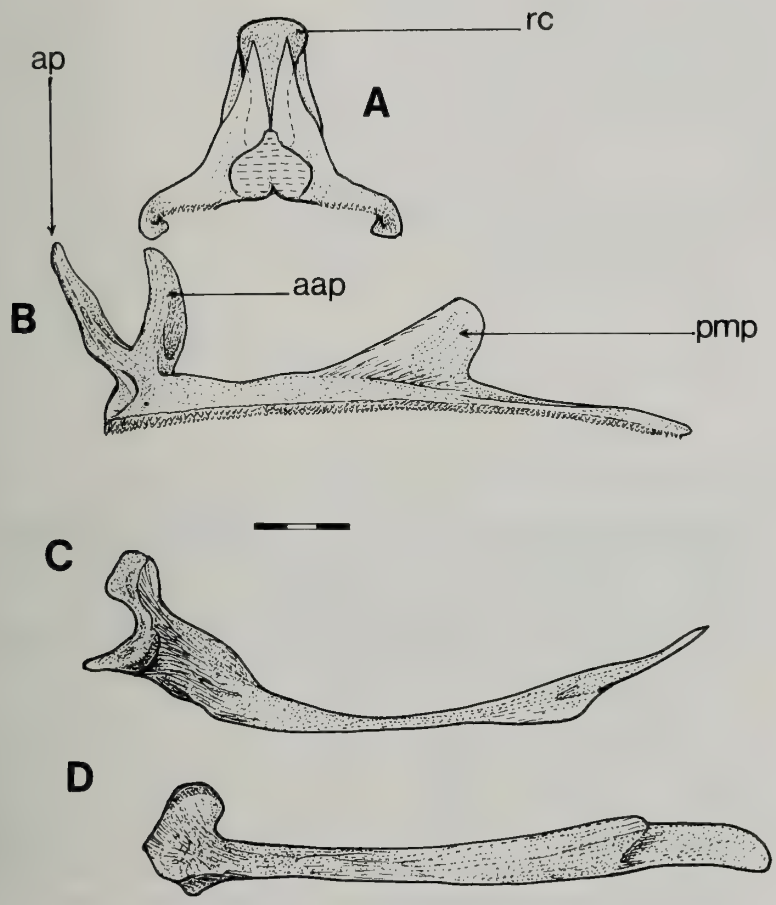

Fig. 10 *Bathygadus melanobranchus* (BMNH 1969.6.26:3227 and following figures). Upper jaw bones: A, symphysial attachment of the premaxillae; B, premaxilla in lateral view; C, maxilla in dorsal view, and D, in lateral view.

Dentaries (d, Fig. 11) angled toward midline and begin to curve anteriorly; bones have strong syndesmotic symphysial connection; coronoid process shallow, rising gently to meet anguloarticular. Posteriorly dentary forked, posterior border of lower branch with long vertical surface abutting anguloarticular. Underside of dentary deeply channeled, medial wall of channel deepening posteriorly, its lateral, open part covered by skin containing five neuromasts. Dentigerous surface narrow, more so on rise of coronoid process; teeth small, conical with inwardly curved tips similar to those of premaxilla arranged irregularly with 4 or 5 in transverse series. Narrow, triangular anterior portion of *anguloarticular* (aa, Fig. 11) articulates between posterior forks of dentary to end in deep articulatory fossa that receives quadrate condyle; lower part of bone almost square, medially with indentation in which lies posterior part of Meckelian cartilage together with minute *coronomeckelian* bone (cm, Fig. 11). Three ligaments link anguloarticular with quadrate, one lateral and two medial. Of the latter, one attaches to anterior, the other to posterior surfaces of quadrate condyle. *Retroarticular* (ra, Fig. 11), J-shaped, occupying posteromedial corner of anguloarticular. *Labial ligament* surrounds the border of lower jaw attaching to distal margin of upper jaw (see Howes, 1988 for detailed description).

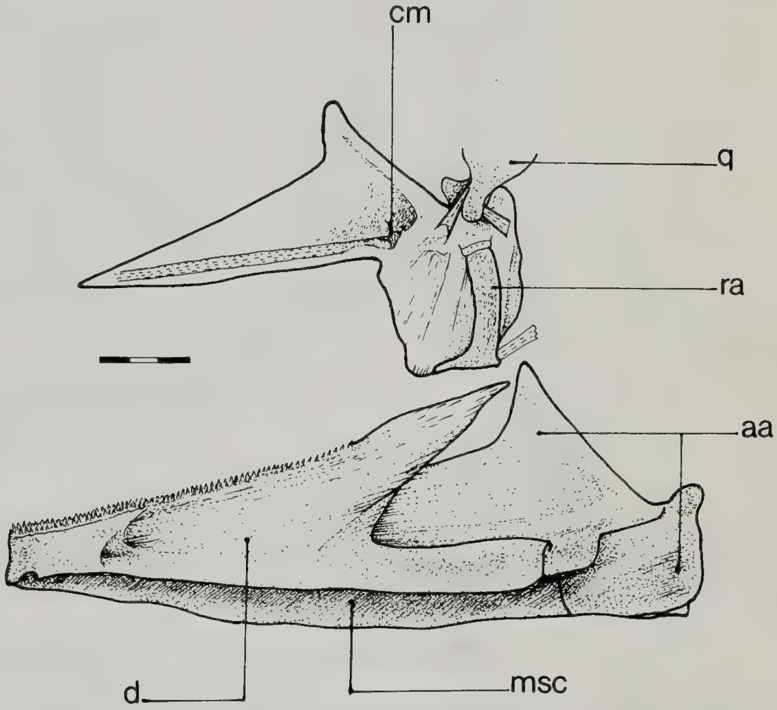

Fig. 11 *Bathygadus melanobranchus*. Lower jaw bones; above, medial view of anguloarticular and retroarticular and their ligamentous connections; below, lateral view of entire jaw.

COMMENTS. Marshall (1966) and Okamura (1970*b*) considered protractile premaxillaries diagnostic for macrouroids. However, 'protractile' is ambiguous. Marshall, comparing the gadoids *Macruronus*, *Lyconus* and *Steindachneria* with macrouroids, noted premaxilla in those taxa to be '... no more than slightly protractile' and '... with rather short pedicels'. For Macrouroidei Okamura gives 'Premaxillary more or less protractile' and for Bathygadinae, 'premaxillary pedicel lower than one-third the length of the premaxillary ramus'; in bathygadids measured the premaxillary ascending process, which is slightly larger than the articular, has variable length (*Bathygadus*, 20.6–31.6%; *Gadomus* 17.8–22.7% pmx ramus). Ascending and articular processes in other gadoids are less than 30% length of ramus. Fahay (1989) noted length of premaxillary ascending process in Steindachneriidae approached that in macrouroids; we measure length as 25% of ramus, which lies within the gadoid range.

Okamura (1970*a*) recognised bathygadids differ from macrouroids in a centrally situated, triangular postmaxillary process of the premaxilla. In macrouroids the process is situated close to, or at the posterior extremity of the ramus

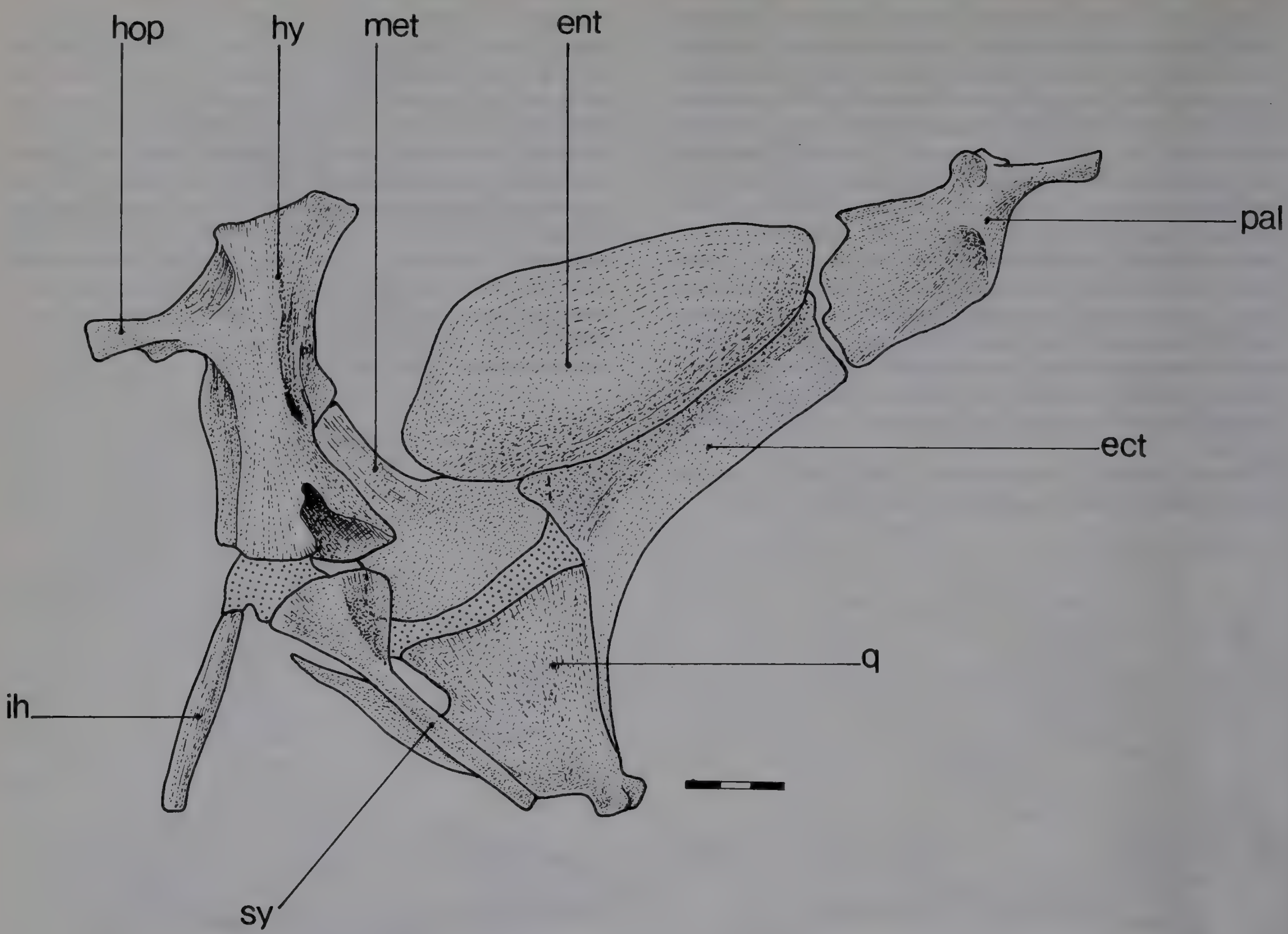

Fig. 12 *Bathygadus melanobranchus*. Palatoquadrate and suspensorial bones in medial view.

and is either blunt or deeply bifurcate posteriorly. In gadoids, position and degree of development of postmaxillary process is variable. Most Moridae possess a broad and posteriorly directed process as in Bathygadidae. In Steindachneriidae the anterodorsal border of the process is rounded and situated centrally on the ramus. The process is small in most Gadidae lacking a marked indentation (gadoid notch of Rosen & Patterson, 1969:401) of its posteroventral border. In Merlucciidae (*Merluccius*) the process is sharply angled posteriorly with a broad and deep notch; in Phycidae it is situated at posterior extremity of premaxilla and may be separated from the ramus by a long shallow notch.

Okamura (1970*b*) recognised a difference between bathygadids and macrouroids where the former has a slender, straight and posteriorly stepped maxilla with a simple articular head. The macrouroid maxilla is convex with an enlarged, complex head and truncated or sloped posterior margin. The general maxillary shape in gadoids is uniformly slender and straight but there is variability in the shape of its distal portion, *viz*. rounded in Moridae, many Gadidae; subtriangular in Merlucciidae, expanded ventrally into a rectangular flange (Phycidae); spade-like (Muraenolepididae). The 'stepped' distal portion of the maxilla of bathygadids is present in Steindachneriidae and Melanonidae. In all these taxa is a well-developed labial ligament (Howes, 1988) with complex fastenings to upper and lower jaws; the posterior portion of the maxilla is anchored by a thickened stump (supramaxillary ligament of Howes, 1988) which fills the 'tread' of the step between the maxillary process and ramus.

In summary, little evidence from jaw morphology supports a relationship between Bathygadidae and Macrouroidei, apart from long premaxillary ascending and articular processes. It is presumably this feature which caused Marshall (1966) and Marshall & Cohen (1973) to list jaw protractibility as one of the characters embracing *Bathygadus* and *Gadomus* with macrouroids. Contrariwise, there are many more resemblances with upper jaws of gadoids, particularly, the large, centrally situated triangular postmaxillary process on the premaxilla.

Palatoquadrate (Figs 12, 13)

Orientation of the palatoquadrate bones is such that anterior articulation with the skull lies at the same level as that of the hyomandibular articulation; dorsal border of palatal and pterygoid bones forms an angle of 45° to horizontal.

Palatine edentulous with almost square, lamellate body (dermopalatine) bearing slight lateral ridge; posterior border is near vertical and articulates with ectopterygoid. Anteriorly, a long process (rostropalatine articulation) extends to overlie maxilla, its base raised into a boss whose medial surface abuts ethmoid cartilage; palatine-premaxillary ligament attaches to anterior surface of boss.

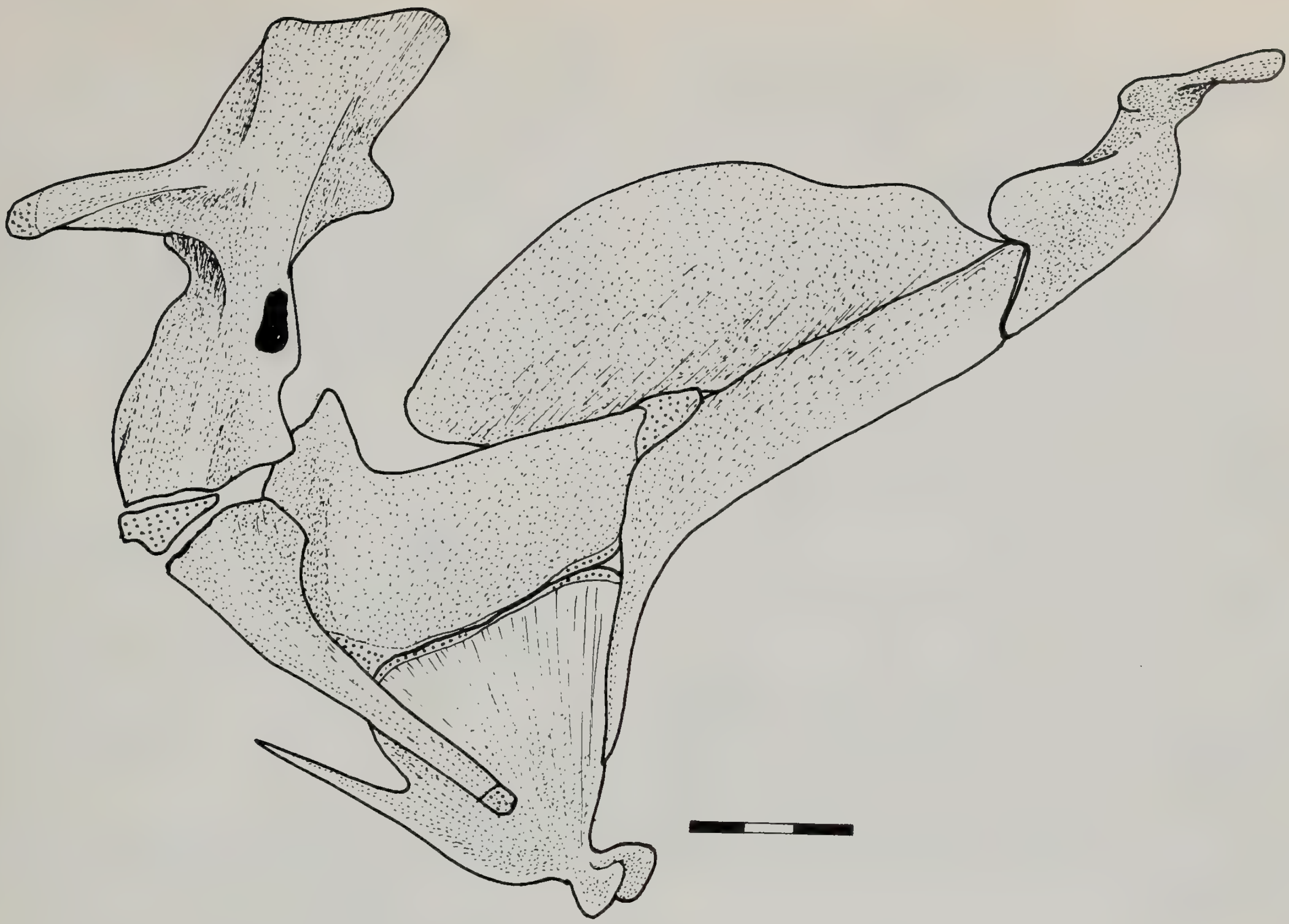

Fig. 13 *Gadomus longifilis* (BMNH 1963.2.25:7–17). Palatoquadrate and suspensorial bones in medial view.

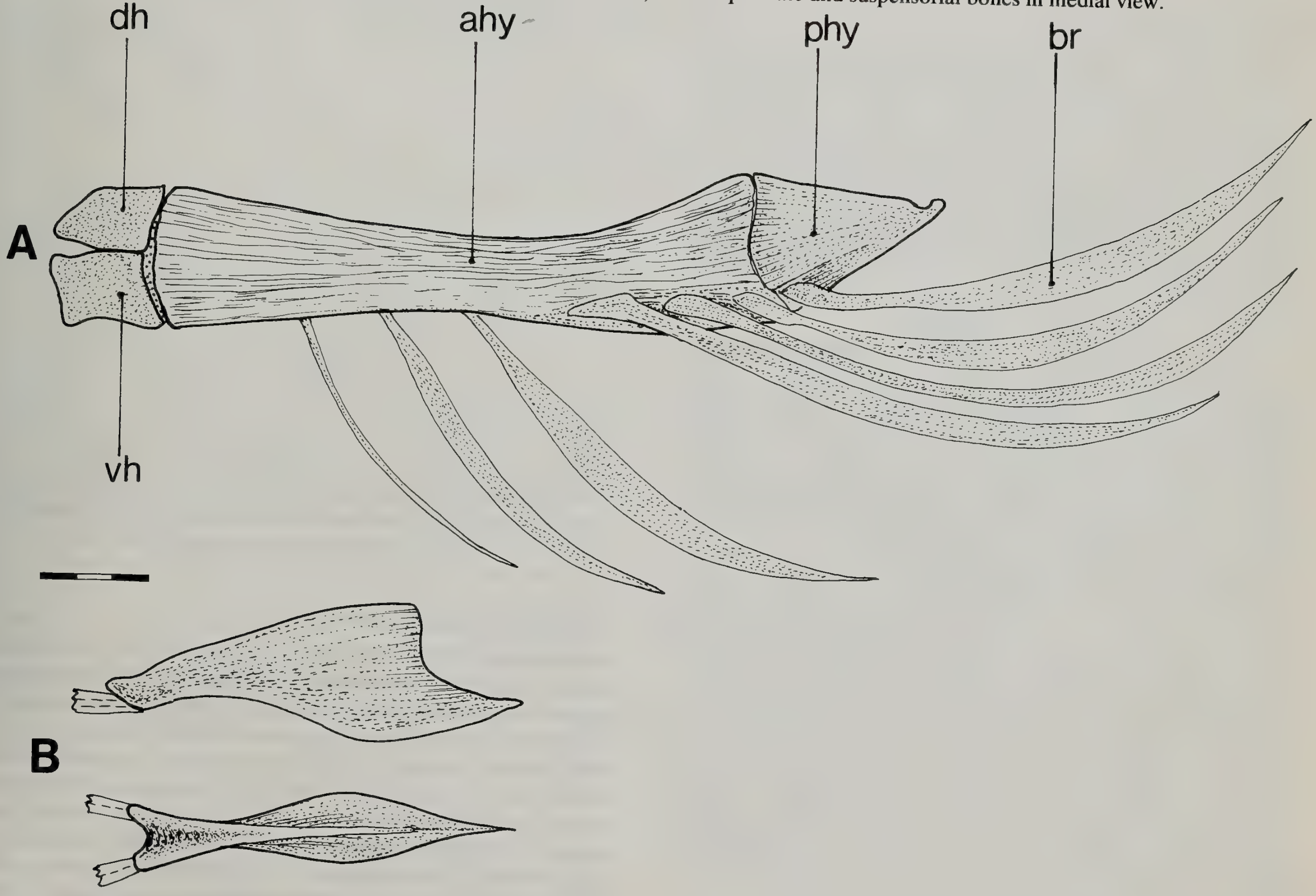

Fig. 14 *Bathygadus melanobranchus*. A, hyoid bar in medial view; B, urohyal in lateral (above) and dorsal (below) views.

Ectopterygoid deep, anterior border meets palatine in vertical synchondral joint; body of bone slopes mesiad at steep angle, posterodorsal tip lying beneath metapterygoid (Fig. 12). Posteroventral stem lies in anterior groove of quadrate. Ventral borders of palatine and ectopterygoid connected to maxilla by broad skin fold.

Quadrate large, trapezoidal; anterior grooved surface articulates with ectopterygoid for almost its entire length; articular condyle broad, deeply indented. Quadrate posterior border contacts metapterygoid *via* strip of cartilage; posteroventral border notched, produced into acuminate strut.

Entopterygoid large, nearly rectangular, sloped mesiad with dorsal border underlying lateral edge of parasphenoid. Posterior border slightly angled, widely separated from hyomandibular. Ventrally, meets meta- and ectopterygoid dorsal borders *via* connective tissue.

Metapterygoid small, axe-shaped having weak attachment to outer flange of hyomandibular and meeting dorsal border of quadrate *via* cartilaginous strip.

COMMENTS. In *Gadomus* the palatine has a strong medial flange and is smaller than in *Bathygadus* (Fig. 13). Gilchrist & Von Bonde (1924) were in error in reporting palatine teeth in *Gadomus capensis* (see Iwamoto, 1986). Among gadoids palatine teeth occur only in Melanonidae. *Gadomus* differs from *Bathygadus* in having a prominent dorsoposterior metapterygoid process and a metapterygoid-hyomandibular space (*cf.* Figs 12 & 13).

Hyoid arch (Figs 12–15)

Hyomandibular with flat outer surface and vertically ridged medial surface; slight depression on dorsolateral face (Fig. 12); anterior border slightly concave, lower part meets metapterygoid; posterior border nearly straight with, dorsally, long, flat posteriorly directed process articulating with operculum. Dorsal articular surface short with slight anterior rise; medial shaft forming body of bone perforated anteriorly and posteriorly for hyoid and mandibular branches of ramus hyomandibularis of facial (VII) nerve. Hyomandibular shaft hollow, allowing passage of mandibular branch of facial which exits from indented medial border.

Symplectic with expanded dorsoposterior surface lying medial to posteroventral edge of metapterygoid contacting, synchondrally, ventral border of hyomandibular. Anterior part of symplectic rod-like, lying medial to ventral surface of quadrate.

Interhyal long, rod-shaped with same length as symplectic shaft. Dorsally articulates with cartilage intervening between ventral border of hyomandibular and symplectic; ventrally articulates with posterior tip of posterohyal.

Dorsohyal and *ventrohyal* small, cone-shaped bones synchondrally joined to one another and to anterior border of anterohyal (Fig. 14); ventrohyals attached ligamentously across midline; dorsohyals separated by basihyal. Anterohyal long, slender with vertical anterior and posterior borders. Posterior part almost rectangular; three *branchiostegal rays* attach to ventral surface and three to ventrolateral face (Fig. 14A). *Posterohyal* slender, triangular with extended posterior vertex articulating with interhyal; anterior border vertical, joining synchondrally with anterohyal. Posterior branchiostegal ray articulates within ventrolateral groove. *Urohyal* (Fig. 14B) small with shallow medial crest whose dorsal surface is produced into triangular plate; ventrally, arrow-shaped.

COMMENTS. Okamura (1970*b*) drew attention to the condition of the dorsohyal in macrouroids where it lies horizontally, making firm midline attachment with its partner. This is not a feature unique to macrouroids; among gadoids a range of conditions is present; almost vertical in Steindachneriidae (Fig. 15A), slightly inturned in Muraenolepididae, Euclichthyidae, Merlucciidae (Figs 15C, E). In Bregmacerotidae, the ventrohyals also contribute to a flat dorsal surface formed by the dorsohyals and are in midline contact so preventing basihyal from extending forward (Fig. 15B); horizontally aligned dorsohyals also occur in Lotidae, Ranicipitidae, Moridae, Phycidae and Trachyrincidae.

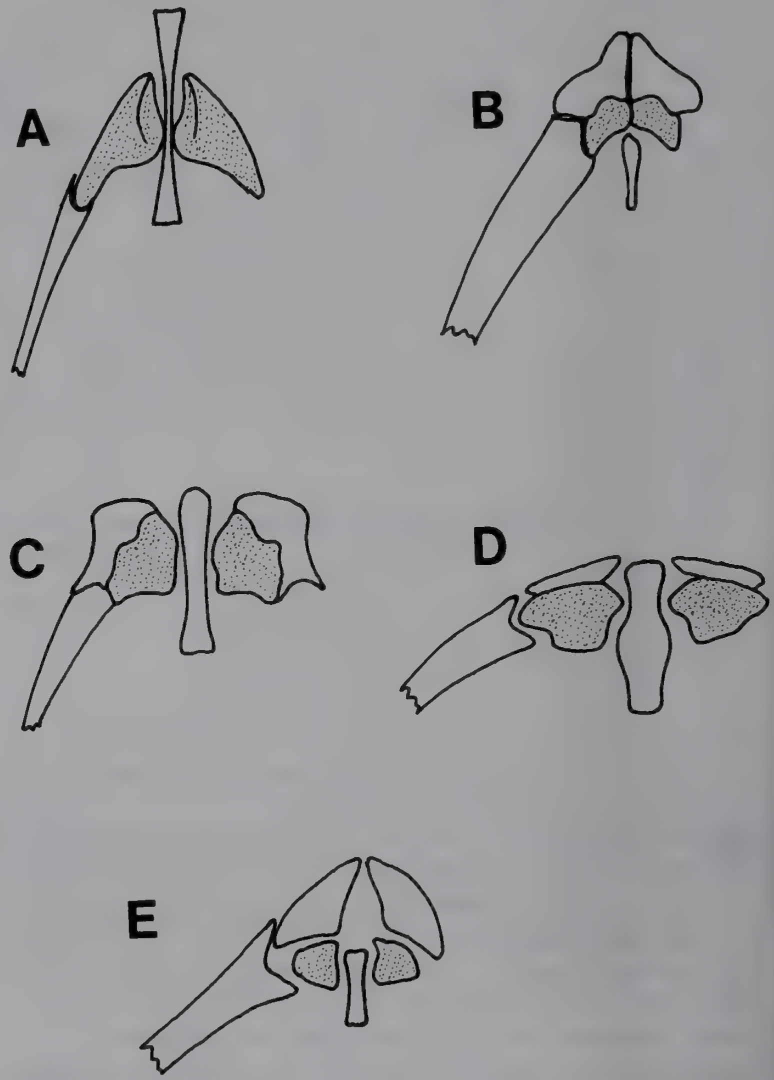

Fig. 15 The relationships of the basihyal to the dorsohyals in A, Steindachneriidae; B, Bregmacerotidae; C, Merlucciidae (*Macruronus*); D, Euclichthyidae; E, Merlucciidae (*Merluccius*). Dorsohyals are shaded, ventrohyals blank.

Opercular series (Figs 16, 17)

Preoperculum large with irregular anterior margin bearing flange along outer border, forming partial roof to sensory canal which contains four neuromasts, two ventrally, one at curvature of bone and one at posterior limb. Ventral part of bone curved mesiad, both posterior and ventral borders fretted. *Suboperculum* flat, ovoid, lying along posteroventral margin of operculum and contacting posterior edge of preoperculum. *Interoperculum* long, shallow, crook-shaped lying medial to preoperculum, its highest point attached to both preoperculum and hyomandibular by dorsally bifurcated ligament (Howes, 1988; 1989). *Operculum* small, triangular

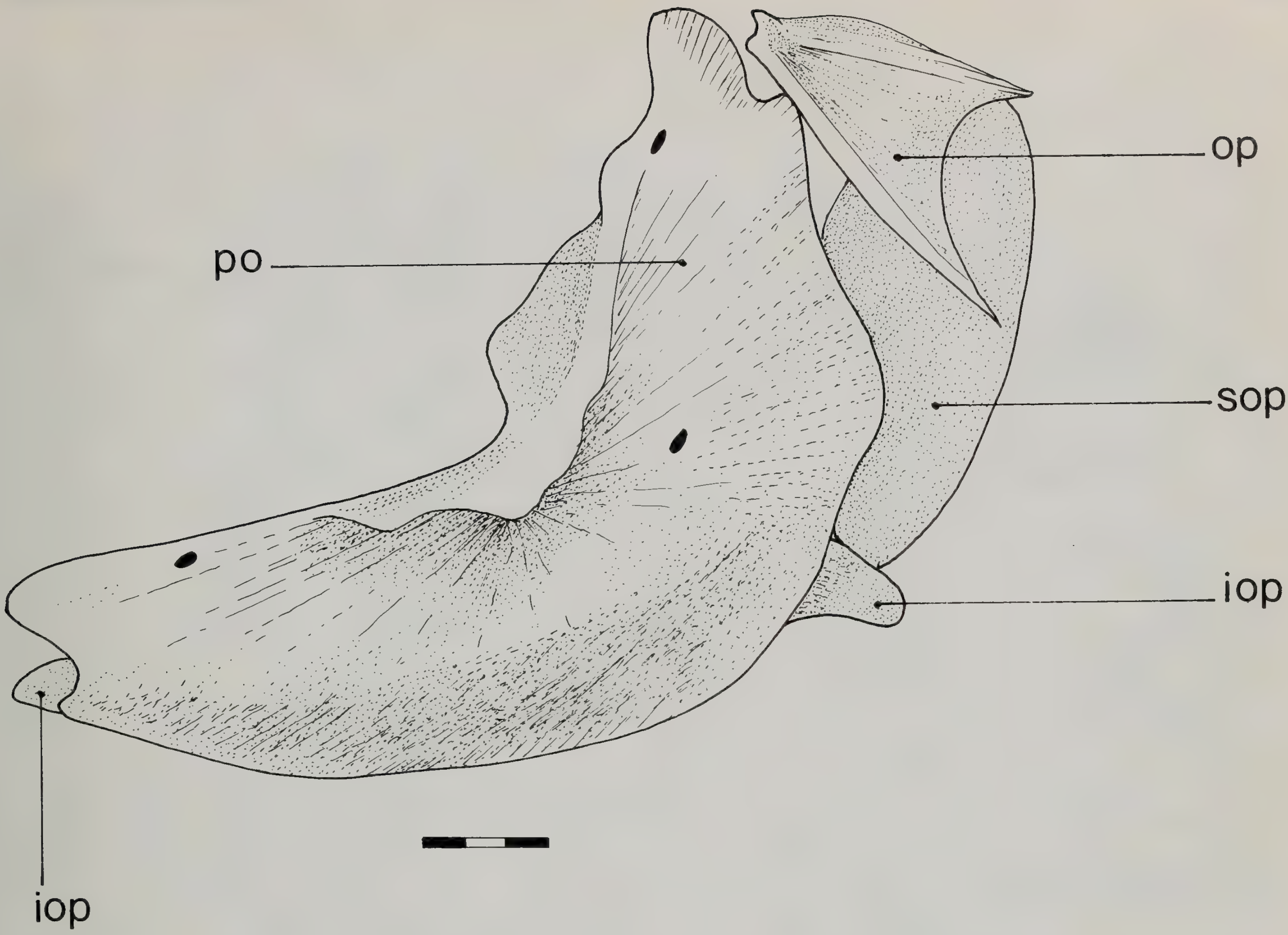

Fig. 16 *Bathygadus melanobranchus*. Opercular series in lateral view.

with markedly concave border, small condyle articulates with hyomandibular opercular process. Two well-developed ridges radiate from condylar part, lower ridge forming preopercular border of bone. Anterodorsal part of operculum lies beneath overhanging posterior pterotic border and restricts maximum elevation of operculum.

COMMENTS. Okamura (1970*b*:51) noted two interopercular morphotypes, one common to *Bathygadus* and some macrouroid genera, the other to *Gadomus* and some other macrouroids. There is a basic difference in shape between the interoperculum of the two genera, that of *Bathygadus* being shallow with a concave ventral margin, that of the latter being deep and more rectangular. However, within *Bathygadus* there is much variation in shape from that of the *Gadomus*-type to the crook-shaped form which Okamura regarded as *Bathygadus*-type (Figs 17, 8–11). Wide variability is not so evident in *Gadomus* (Fig. 17, a-k). As well as occurring in some macrouroids, the *Bathygadus* interopercular morphotype is present in the bythitoid *Lamprogrammus* (Fig. 171), so it seems that similar interopercular shapes may not be reliable as indicators of phylogenetic relationship, but rather reflect functional demands.

In *Bathygadus* a wide space occurs between the preoperculum and operculum covered by the black membrane lining the bones' inner surfaces. In common with gadoids the operculum is separated from the preopercular border whereas in macrouroids it is overlapped by the preoperculum (Okamura, 1970*b*). An interosseus space occurs between symplectic and preoperculum, a feature common to gadoids; in macrouroids the area is occluded by symplectic expansion.

Branchial arches (Fig. 18)

Medial, basal branchial arch elements comprise a narrow-waisted, ossified *basihyal*, posteriorly overlapped by arrow-shaped 1st *basibranchial* comprising ossified plate overlying thin cartilaginous rod; fully ossified large pyriform 2nd basibranchial, and a medial cartilage lying between 4th hypobranchials. The latter are long, 1st *hypobranchial* with four slender gill-rakers along outer margin and six, club-shaped rakers along inner; 2nd hypobranchial with six outer and five inner (denticulate) rakers; 3rd short, with two or three large denticulate outer rakers.

Ceratobranchials elongate, 1st with 16–17 long, spear-like outer rakers, 12–14 club-shaped, denticulate inner rakers; 2nd, 3rd and 4th each with 10–12 large club-shaped outer and inner rakers; 5th narrowly triangular with concave underside, toothed surface bears numerous, short, conical teeth with slightly posteriorly curved tips. First *epibranchial* with 6–7 long, slender outer rakers, 3–4 club-shaped, denticulate inner rakers; 2nd with 3 outer and 3 inner; 3rd and 4th each with 2 outer and 1 inner raker. Each epibranchial bears an uncinate process. Epibranchial 3 bears a long, near rectangular tooth plate along its medial surface. *Pharyngobranchials* number

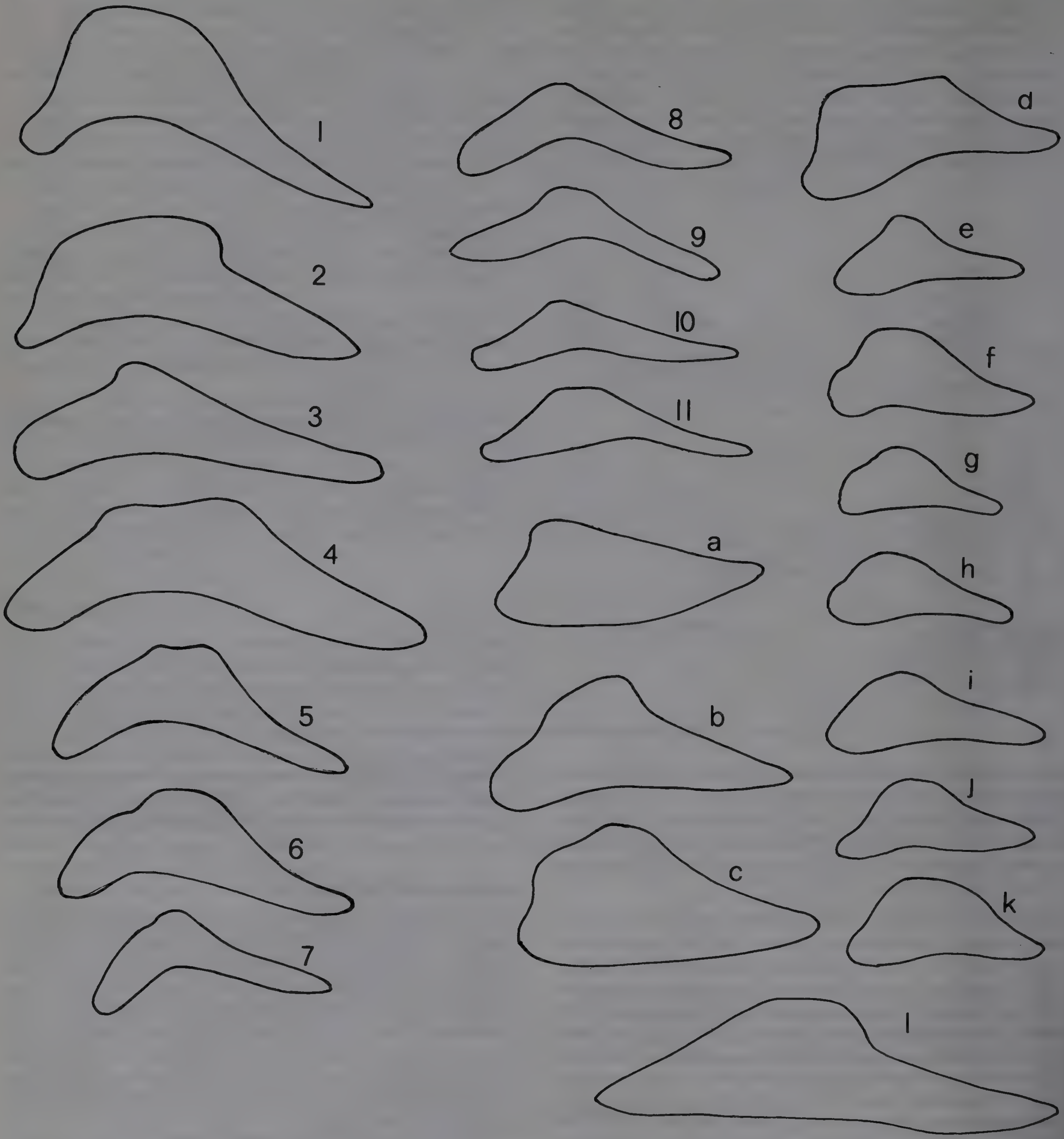

Fig. 17 Interopercular shapes in *Bathygadus* (1–11), *Gadomus* (a–k) and the ophidiiform *Lamprogrammus niger* (1). 1, *B. cottoides*, 2, *macrops*, 3, *favosus* 4, *melanobranchus* 5, *sulcatus*, 6, *nipponicus*, 7, *bowersi*, 8, *spongiceps*, 9, *entomelas*, 10, *filamentosus*, 11, *antrodes*; a, *G. multifilis*, b, *capensis*, c, *arcuatus*, d, *furvescens*, e, *longifilis*, f, *colletti*, g, *melanopterus*, h, *micronema* (type; = *melanopterus*), i, *introniger*, j, *denticulatus*, k, *magnifilis*.

three; 1st small, cartilaginous and lunate; 2nd and 3rd large, ossified each bearing tooth-plates (two plates on 3), teeth moderately developed, conical, curved mesiad. *Interarcual cartilage* small, lying in collagenous strand linking 1st and 2nd pharyngobranchials (Travers, 1981).

Gill-rakers (Fig. 18B–D) on outer margin of 1st ceratobranchial, thin, blade-like, forward facing margin of raker bearing irregular rows of conical denticles. Almost always a single, dorsally directed denticle at tip of raker (Fig. 18B), no denticles on raker's posterior margin. Club-shaped rakers

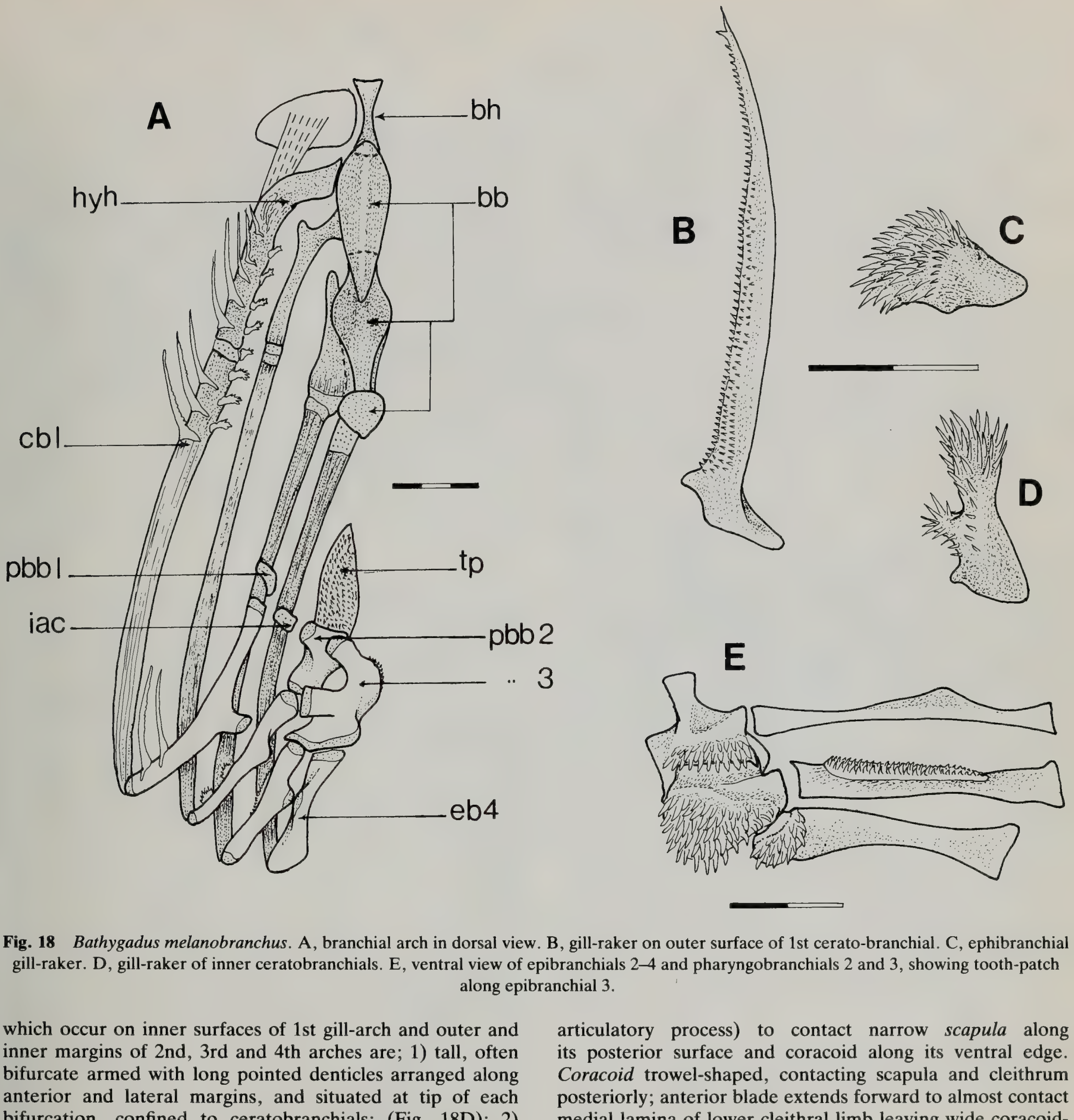

Fig. 18 *Bathygadus melanobranchus*. A, branchial arch in dorsal view. B, gill-raker on outer surface of 1st cerato-branchial. C, ephibranchial gill-raker. D, gill-raker of inner ceratobranchials. E, ventral view of epibranchials 2–4 and pharyngobranchials 2 and 3, showing tooth-patch along epibranchial 3.

which occur on inner surfaces of 1st gill-arch and outer and inner margins of 2nd, 3rd and 4th arches are; 1) tall, often bifurcate armed with long pointed denticles arranged along anterior and lateral margins, and situated at tip of each bifurcation, confined to ceratobranchials; (Fig. 18D); 2) short, wide with sloped outer and rounded inner margin, armed with cluster of pointed denticles, confined to epibranchials (Fig. 18C).

Pectoral girdle (Fig. 19)

Supracleithrum splint-like, slightly expanded distally with smooth rounded surface articulating with distal depression of posttemporal; lies at 45° angle to cleithral limb. *Cleithrum* with short, upright upper limb and long narrowly pointed lower limb angled at 55° to horizontal. Posterior lamina of upper part broadly triangular with ventromedial cleft from whose base a narrow lamina extends horizontally (scapular articulatory process) to contact narrow *scapula* along its posterior surface and coracoid along its ventral edge. *Coracoid* trowel-shaped, contacting scapula and cleithrum posteriorly; anterior blade extends forward to almost contact medial lamina of lower cleithral limb leaving wide coracoid-cleithral aperture.

Baudelot's ligament runs from upper medial surface of supracleithrum to turn immediately posteriorly, loop around dorsal tip of cleithral limb then pass anteromedially and downward beneath epaxial muscle mass to attach to 1st centrum (Figs 19 & 25).

A single *postcleithrum* extends ventroposteriorly, firmly attached to hypaxial musculature (Fig. 25). *Actinosts* number 5 in *Bathygadus melanobranchus* and *B. favosus* (3 in *B. antrodes*, (Okamura, 1970*b*) and *B. melanobranchus*; 14–17 fin rays articulate with actinosts.

COMMENTS. Okamura (1970*b*:93) noted variability among

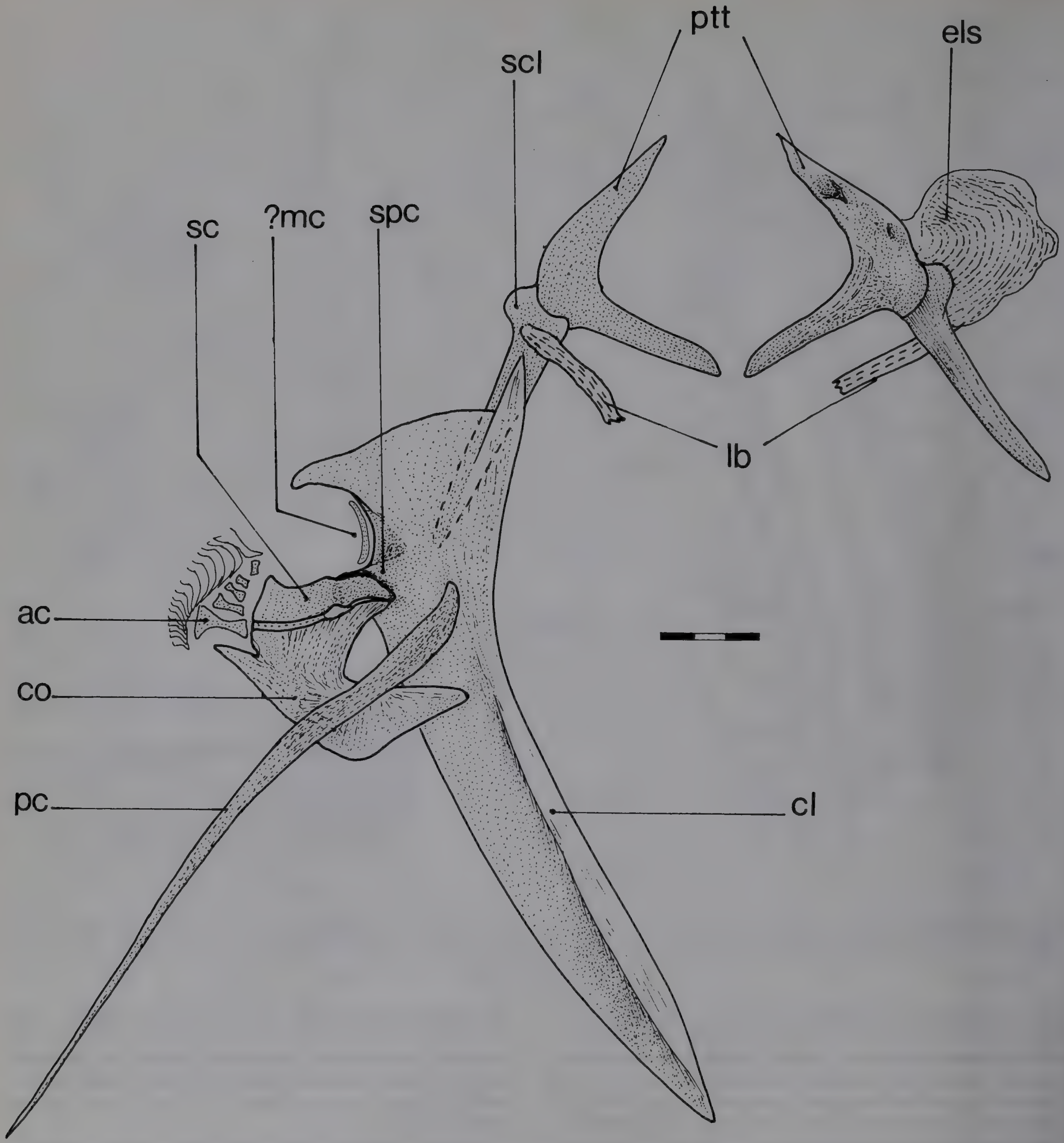

Fig. 19 *Bathygadus favosus*. Pectoral girdle and posttemporal in medial view and (above right) lateral view of posttemporal with enlarged lateral line scale.

gadoids of the placement of the scapular foramen. In macrouroids and most gadoids it lies between the scapula and coracoid as in *Bathygadus melanobranchus*, *B. favosus* and *Gadomus longifilis*; in *B. sulcatus*, *B. filamentosus* and *G. melanopterus* it lies within the scapula (Gilbert & Hubbs, 1916) and in *B. antrodes* almost entirely within the scapula (Smith & Radcliffe, 1912). A brief survey among gadoids shows the foramen lies between the scapula and coracoid in all families, although in the two examined morid genera *Lepidion* and *Physiculus* it lies within the scapula (see also Regan, 1903:463). The size of the medial cleithral lamina which contacts the scapula may have classificatory relevance being well-developed in Bathygadidae, Moridae and Trachyrincidae; in most gadoids it is usually absent and only slightly developed in Lotidae, Merlucciidae and Gadidae. In *Bathygadus melanobranchus* an oblong cartilage lies along the cleithral border of the scapula (?mc Fig. 19) which may represent a mesocoracoid, otherwise lacking in gadoids.

Posttemporal (Figs 3, 6, 19)

Posttemporal is boomerang-shaped, its dorsal limb attaching to epioccipital summit, its narrow ventral limb ligamentously to lateral process of intercalar. Passing between the limbs is a broad segment of *epaxialis* muscle which inserts on pterotic (Fig. 25). A small V-shaped opening occurs near junction with supracleithrum and is narrowly separated from wide aperture extending across width of limb. Running along anterior border of posttemporal is main branch of *ramus lateralis accessorius* (RLA) nerve; pectoral-pelvic branch of nerve detatches from main trunk, crosses dorsal face of posttemporal and runs down posteromedial border. Ventrally, posttemporal attaches to rounded upper part of supracleithrum *via* cartilaginous meniscus.

Anterolateral to posttemporal lie one or two thin, gutter-like elements containing neuromasts which provide a posterior continuation of pterotic sensory canal linking it with the enlarged scale (see below) of the lateral line. These elements are identified as *extrascapulars*; their large, open canal appears to have no connection with the small posttemporal canal.

COMMENTS. Association between the posttemporal and lateral cranial wall is variable in gadiforms. In all macrouroids examined and *Trachyrincus* the lower limb of the bone is broad, flat articulating firmly and broadly with the intercalar. The pterotic extends backwards to contact the lower limb (sometimes leaving only a small ventral gap) thus forming a solid wall. This type of contact is present in some gadoids, eg. *Molva*, *Lota*, *Brosme* (all Lotidae), there is only partial contact of pterotic with posttemporal limb, the extrascapulars intervening laterally between the pterotic and posttemporal. Posttemporal morphology in Merlucciidae, Moridae, Ranicipitidae, Melanonidae and Steindachneriidae resembles the (presumed plesiomorphic) condition of Bathygadidae where the lower limb is slender, cylindrical and contacts the intercalar cartilaginously. *Trachyrincus* possesses a unique condition, *viz*. posttemporal bears extensive medial lamina contacting exoccipital (Regan, 1903:462).

An *enlarged scale* (els, Fig. 19) attaches to the posterior border of the posttemporal with often, a smaller scale lying partly beneath it. The enlarged scale has a single neuromast served by a branch of the lateral line nerve which passes medial to its lower border. Okamura (1970*b*:16) considered similar scales in macrouroids as being so modified as not to be regarded as scales. There is no evidence which suggests they are not merely enlarged lateral line scales. Such scales occur in (? all) taxa belonging to the macrouroid subfamily Macrourinae and some ophidiiforms (p. 185).

Pelvic girdle (Fig. 24B)

Pelvic girdle comprises two V-shaped *pelvic bones*, each with strongly developed, medially directed postpelvic process; the right always slightly overlaps the left, both are connected by thick ligament. Anteriorly bones are separated from one another and from cleithral symphysis of pectoral girdle by median cartilage. Halfway along each pelvic bone a ligament connects its lateral face with medial border of lower cleithral limb. Outer edge of pelvic bone bears up-turned spine-like process which attaches to tendinous *hypaxialis* muscle. Posterior corner of pelvic base with long facet for articulation with eight or nine pelvic fin rays; all rays have triangular 'hammer-head' proximal articular surfaces; outer ray thickened and short; 2nd ray thickened, filamentous in *Gadomus*.

In *Bathygadus* the 'pelvic spine' is a solid bony process not to be confused with 'pelvic splint' or 'spinelet' common in other teleosts. Okamura (1970*b*:98) noted the 'spine' in *Gadomus* which he considered homologous with the 'mid-pelvic process' of macrouroids. A lateral pelvic process is widespread in gadoids and macrouroids but never so prominently anterodorsally directed as in Bathygadidae.

The tendinous connections between pelvic girdle and cleithrum are more complex than depicted by Okamura (1970*b*:95); a wide, medial tendinous band extends backward from the cleithral symphysis to join a diagonal, cylindrical tendon running from the ventromedial cleithral surface to the anterodorsal surface of the pelvic bone. Thick, darkly pigmented connective tissue covers the triangular space between the tendons; hypaxial and pelvic muscles insert on medial tendinous band.

Vertebral column (Fig. 20)

Bathygadus has 12–14 (rarely 13 or 14) abdominal and *ca* 70 caudal vertebrae, ie. those with closed haemal arches. *Gadomus* has 12–13 abdominal and always more than 80 caudal vertebrae.

In *Bathygadus* the first three centra bear stout, blunt neural spines whose tips are widely divergent from one another; the first narrowly separated from supraoccipital crest, its anterior surface grooved (doubtless due to contraction of longitudinal body musculature, the supraoccipital is forced back into this groove). A pair of neural zygapophysis on 1st centrum articulate with paired exoccipital condyles. Each successive neural spine with more finely pointed tip until from 7th or 8th they become slender, needle-like. Pre- and postzygapophyses present posteriorly from 17th–18th vertebrae; 5th–11th vertebrae bear broad, lateral parapophyses each bearing a rib, 6th–10th parapophyses successively broader, diminishing in width from 11th–14th and replaced by haemal spine on 14th. *Epipleural ribs* 4–8 from 3rd to 10th vertebrae. Caudal vertebrae elongate, narrow-waisted with low-angled neural and haemal arches and spines; spines of more caudal elements with marked posterior curvature causing them to lie almost horizontally.

COMMENTS. Okamura (1970*b*:110) noted in macrouroids the absence of neural and haemal spines from the last four vertebrae. In all bathygadids examined, neural and haemal spines are present on all caudal centra.

Dorsal and anal fins and supports (Fig. 20)

Bathygadus and *Gadomus* have two *dorsal fins*, 1st with 2 spines, 6–12 soft rays; 2nd with *ca* 100+ soft rays. First dorsal fin spine small, lying adnate to anterior base of long 2nd dorsal spine, spines supported by single narrow radial; following *ca* 13 radials diminish in length and stoutness, numbers 2–10 support fin rays, the following three or four radials do not support rays; 14th or so radial followed by another much stouter of nearly same length as 2nd supporting 1st ray of second dorsal fin. *Anal fin* lacks stout spine, composed of soft rays supported by slender radials with cartilaginous proximal tips. There are no supraneurals.

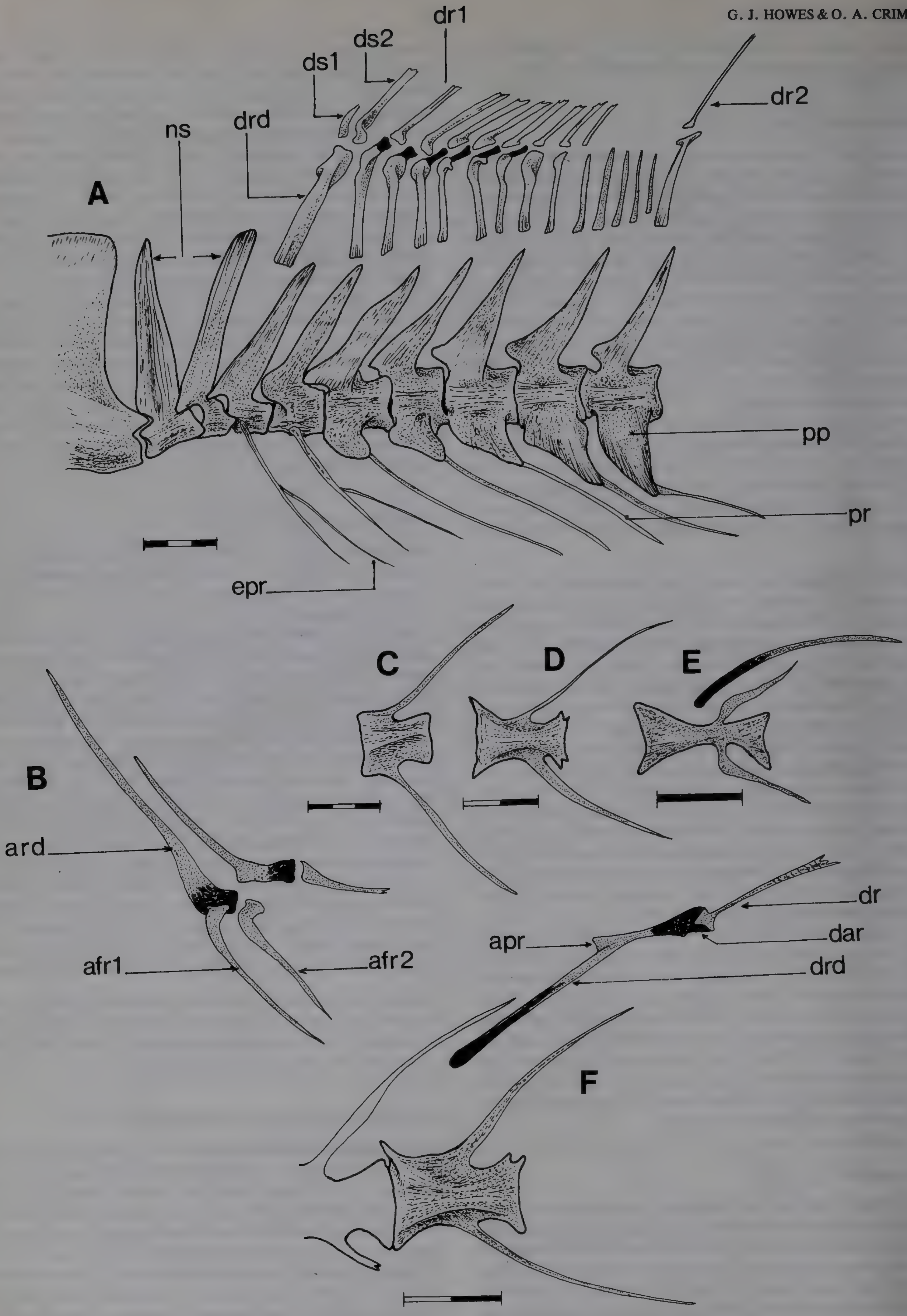
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Fig. 20 *Bathygadus melanobranchus*. Anterior region of vertebral column with dorsal fin supports *in situ*. B, anterior supports of the anal fin. C–F, vertebrae; C=19th, D=39th, E=60th and with associated radial, F=35th with associated dorsal radial. Cartilage shown as solid black.

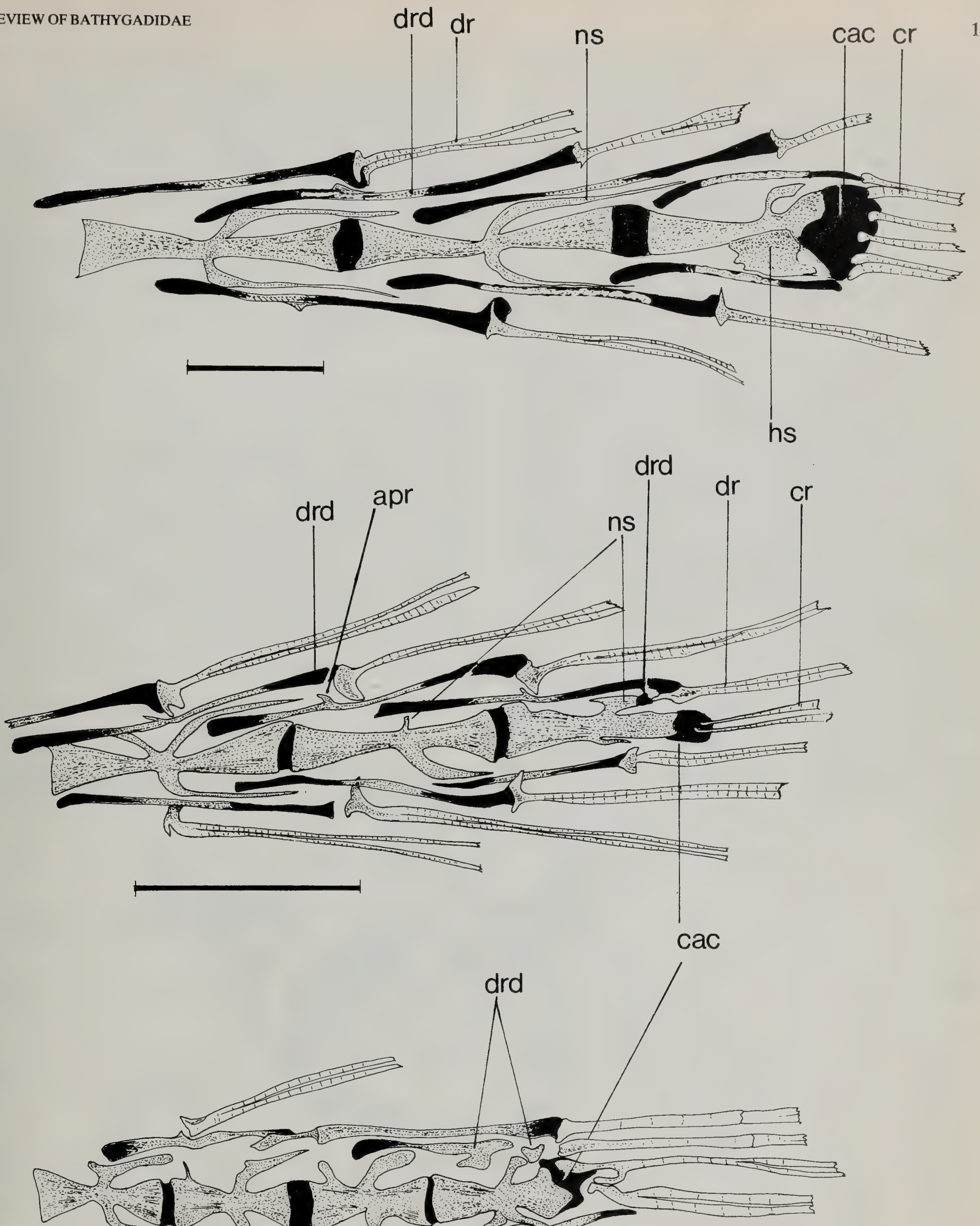
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Fig. 21 Caudal fin region of; A, *Bathygadus melanobranchus*, B, *B. macrops*; C, *Gadomus arcuatus*. Cartilage is shown as solid black. Scale bars=1mm.

Fahay & Markle (1984, table 75) give 8–13 1st dorsal rays for *Bathygadus* and 11–14 for *Gadomus*. In specimens examined there are no more than a total of 12 rays in the former and 13 in the latter. Both posterior dorsal and anal fin radials bear, posterodorsally, a spine-like process which articulates with the distal cartilaginous radial supporting the preceding fin ray.

In macrouroids the first few radials of the anal fin lie well forward, below the 9th or 10th abdominal vertebrae rather than the posterior abdominal or 1st caudal as in the Bathygadidae and other gadoids; the exception among macrouroids is *Hymenocephalus* which retains the plesiomorphic gadoid condition (Okamura, 1970*b*:108). In *Trachyrincus* three or four anal radials lie beneath the last abdominal and 1st caudal vertebrae and do not form the anteroventral arc arrangement characteristic of macrouroid anal radials.

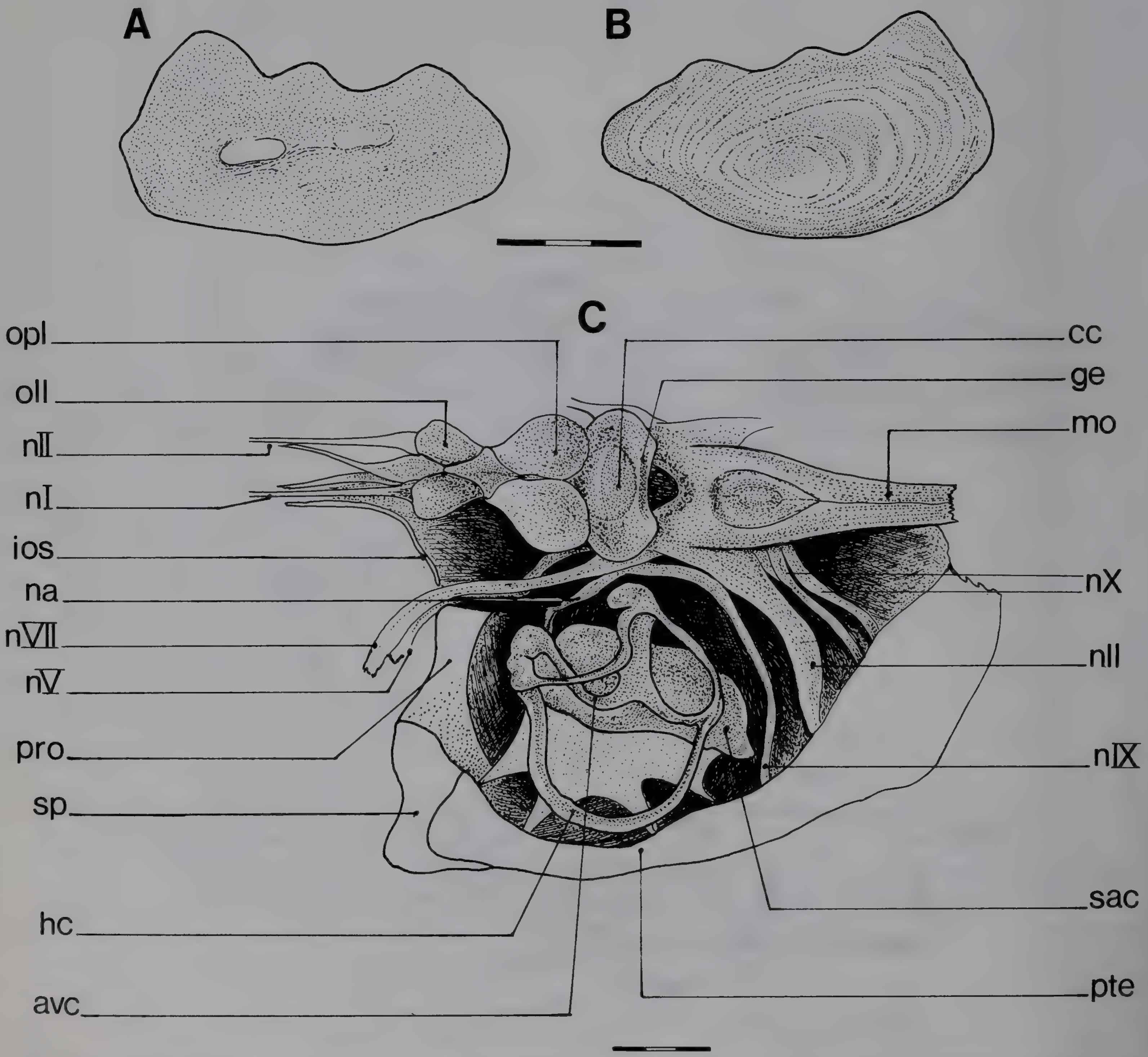

Fig. 22 *Bathygadus favosus*. The inner ear and brain. Above, otolith showing A, inner, and B, outer surfaces; C, dorsal view of inner ear and brain.

Caudal 'skeleton' (Fig. 21)

Like macrouroids, bathygadids display no distinct caudal fin, the tail terminating in 4 or 5 long filamentous rays. The internal structure of the tail is simple although there is some variability with regard to neural and haemal spines and radials (see below). There is no true caudal skeleton and the 'caudal' rays seem derived either from dorsal and/or anal rays which surround the terminal centrum. The last centrum is never complete, its posterior part terminating in a flat cartilaginous plate supporting 2–4 rays. The neural spine of the last vertebra may be normal shape (Fig. 21A), elongate and lamellate (Fig. 21B) or shortened (Fig. 21C); the haemal spine is similarly modified. The last radial may be posteriorly expanded as in *Gadomus arcuatus* (Fig. 21C).

COMMENTS. Okamura (1970*b*) considered a normal macrouroid caudal skeleton one in which each ray is supported by a radial (interneural of Okamura), and a regenerated caudal (or pseudocaudal) one in which a large cartilaginous plate, derived from intervertebral cartilage, supports caudal rays. All bathygadids examined fall into this latter category and since there are no obvious breaks in the radials or other distortions which suggest breakage it is difficult to ascertain which is normal and which is regenerated caudal skeleton. Presumably, when the tail is broken off in life, breakage occurs intervertebrally so a 'caudal' cartilage will develop from the intervertebral one. Compared with *Melanonus*, *Steindachneria* and *Trachyrincus* in which caudal elements are identifiable (see respectively, Paulin, 1983; Fahay, 1989; Howes, 1989) the caudal fin of bathygadids is reductive, in which it resembles macrouroids.

Brain
Fig. 22

The bathygadid brain is elongate and shallow, filling central area of cranial cavity; olfactory bulbs lie midway between lateral ethmoid and olfactory lobes being situated within paired cavities formed by frontal ventral laminae and extensions of medial septum (p. 163). Olfactory tracts thin, narrowly separated from one another posterior to olfactory sac. Olfactory lobes ovoid, separated from optic lobes by shallow fissure. Optic nerves thin, feeble, crossing one another anterior to olfactory lobes. High cerebellar corpus bordered by ovoid granular eminences. Inferior lobes prominent, hypophysis large, almost spherical. High posterior cerebellar crests. Trigeminal and facial trunk emanates from below cerebellar corpus; acoustic nerve stems from above root of trigeminal trunk, turns dorsad, branching into two rami serving anterior ampullae of inner ear canal.

COMMENTS. Okamura (1970*b*:73) noted olfactory lobes in macrouroids are 'spherical or ovoid in shape and considerably well developed'. Observations on at least one taxon of each gadoid family indicate that gadoid olfactory lobes are larger than macrouroid, as they are in bathygadids. Anterior placement of olfactory bulbs has been considered diagnostic of Gadiformes (Svetovidov, 1948). Olfactory bulb position is, however, variable; in *Bathygadus* they occur between forebrain lobes and olfactory sacs, in *Gadomus* they lie close to the brain. In macrouroids, the bulbs lie within the nasal cavity in Macrourinae but in Macrouroidinae are close to the brain (this is considered the plesiomorphic position since it is the condition of most teleosts). Among gadoids the bulbs lie close to the brain in Melanonidae, Euclichthyidae and Ranicipitidae; occupy an intermediate position in *Lyconus* (Merlucciidae); lie close to nasal sac, but posterior to lateral ethmoid in Moridae, Gadidae, Phycidae (? all) and Muraenolepididae; and within nasal cavity in other merlucciid genera *Merluccius* and *Macruronus* (condition in *Lyconodes* unknown). In Steindachneriidae and Merlucciidae the olfactory bulbs migrate forward during ontogeny (Inada, 1981; Fahay, 1989) which suggests that an ontogenetic shift has occurred independently

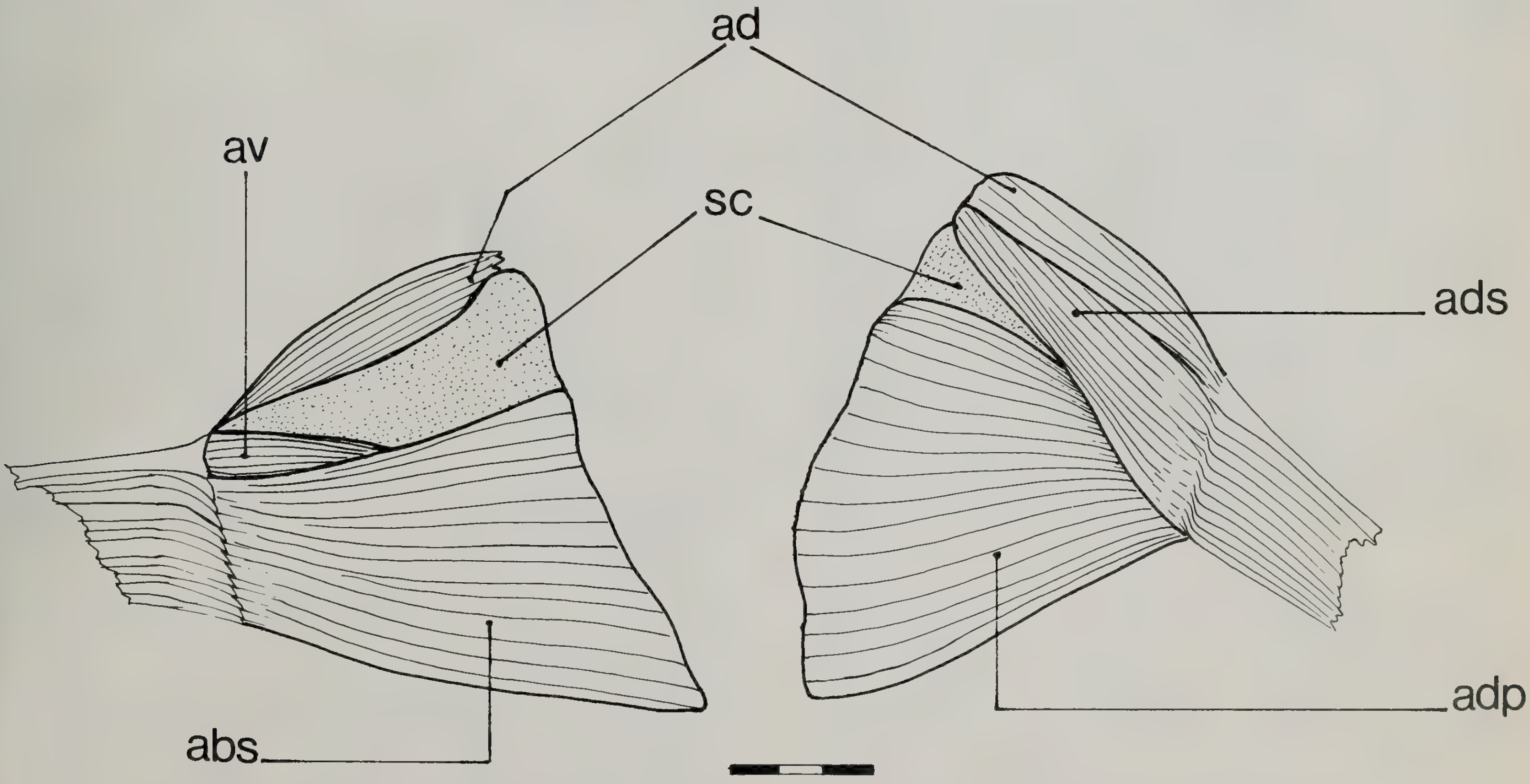

Fig. 23 *Bathygadus favosus*. Muscles of the pectoral girdle; left, lateral; right, medial view.

in various gadoid and macrouroid lineages (Howes, 1989). According to Fahay (1989), in *Steindachneria*, the olfactory lobes migrate forward to become olfactory bulbs; this is perplexing since in all specimens we have examined, olfactory bulbs and lobes are distinct entities. In Bathygadidae the olfactory tract is simple and undivided whereas in macrouroids and many gadoids it comprises two or more strands. The optic lobes are relatively small compared with those of other gadoids.

Swimbladder

Swimbladder; simple, elongate sac extending to above anus containing 2 retia mirabilia in *Bathygadus*, 4 in *Gadomus*; no drumming muscles.

COMMENTS. Okamura (1970*b*:115–7) describes a pair of muscle bands extending from the auditory bullae (intercalar) to between 4th and 7th vertebrae. No muscles in this position have been found in any bathygadid, macrouroid or gadoid examined and it appears Okamura has misinterpreted as drumming muscles the *retractor dorsalis* which run from those vertebrae to the pharyngobranchials (Howes, 1988).

Intestine

Intestine S-shaped coil in *Bathygadus* and *Gadomus*. Okamura (1970*b*) recognised this pattern as primitive for macrouroids; more derived patterns involve 4–6 loops or spirals (eg. *Squalogadus* (Macrouroidinae)).

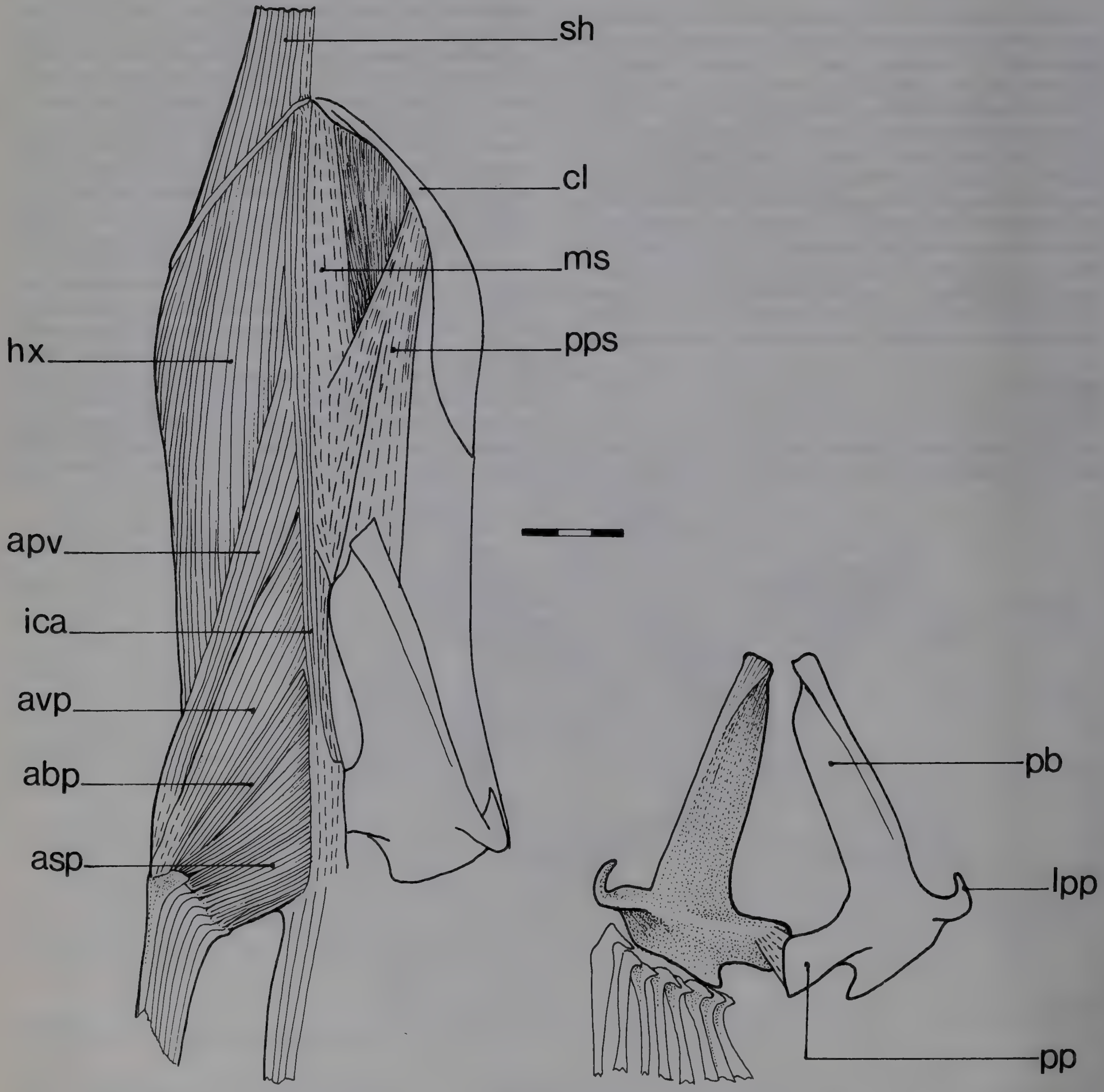

Fig. 24 *Bathygadus favosus*. A, muscles of the pelvic girdle; B, bones of the pelvic girdle in dorsal view.

Gill-filaments

Gill-filaments of *Bathygadus* and *Gadomus* are short, 20–25% of outer gill-raker length (measured against longest raker on ceratobranchial); exceptionally, *B. macrops* has filaments of equal length to rakers.

COMMENTS. Among gadoids short gill-filaments occur only in Merlucciidae (*Merluccius*); Inada (1981, fig. 47L) illustrates this example in *M. australis*, even so the filaments of this species are short compared with other *Merluccius* (equal to gill-raker length, those in other species longer than rakers) and still longer than those of bathygadids. Short gill-filaments have not been found in macrouroids but occur in some Bythitoidei, *viz. Abyssobrotula*, *Acanthonus*, *Bassogigas*, *Bassozetus*, *Glyptophidium* and *Lamprogrammus*. In these taxa it is usually only the outer arch filaments that are reduced, those on the inner arches being twice as long. In bathygadids reduction of filaments on all gill-arches is considered to be a derived feature for the family.

Myology

Muscles and ligaments of the head have been described by Howes (1988); here is given a more complete description of branchial arch muscles together with descriptions of pectoral and pelvic girdles and axial skeleton.

Branchial arch muscles

Obliqus ventralis muscles of 1st and 2nd gill-arches were referred to by Howes (1988; 1989) as 'reduced'. This ambiguous term means that the muscle is almost entirely tendinous, in some taxa comprising only a tendon without muscle fibres. Attachment to ceratobranchial is at its articulatory (with hypobranchial) margin, rather than a distance along it as in other teleosts. *Bathygadus melanobranchus* lacks muscle and tendon from 1st arch, 2nd bears reduced muscle body; a similar condition occurs in *Gadomus 'multifilis'* and *G. longifilis*.

Pectoral girdle muscles (Fig. 23)

Abductor superficialis spans proximal part of scapula and coracoid, originates from dorsomedial rim of cleithrum; insertion on each fin ray, other than 1st, *via* tendon. *Arrector ventralis* originates from lateral face of coracoid, and ventromedial area of cleithral rim; mostly covered by abductor, inserts tendinously on dorsomedial aspect of 1st pectoral ray. *Adductor profundus* originates from coracoid, inserts tendinously on pectoral rays. Dorsally and partially medial to profundus lies *arrector dorsalis*, and *adductor superficialis*, both originating from medial posteromedial border of cleithrum, barely separable from one another, the latter identified by its insertion to the medial aspect of the 1st pectoral ray; the latter inserting on bases of all other rays.

Pelvic girdle muscles (Fig. 24)

Abductor superficialis pelvicus originates from midline septum, inserts on all pelvic rays. *Arrector ventralis pelvicus*, narrow, tendinous and continuous medially with *infracarinalis anterior*, inserts on ventrolateral aspect of 1st pelvic ray. *Adductor profundus pelvicus* runs from midline septum, inserts on outer pelvic ray. *Arrector dorsalis pelvicus* extends from midline septum of *hypaxialis*, inserts tendinously on anteriorly directed lateral pelvic process (p. 175). *Abductor profundus pelvicus* stems from midline raphe, loosely attached to pelvic girdle by connective tissue, inserts on bases of all but 1st pelvic ray.

Dorsal pelvic musculature comprises *adductor superficialis pelvicus*, extends from midline raphe inserts tendinously on all rays; *adductor profundus pelvicus*, narrow, tendinous, originating with former muscle, its more posterior fibres stem from ventrolateral margin of pelvic bone, inserts on 1st ray and heads of the three outer soft rays.

Anterior body muscles (Fig. 25)

Supracarinalis anterior runs from anterolateral face of 1st radial to supraoccipital crest; muscle deepens at attachment to dorsal radial and immediately joins an aponeurosis with fibres stretching mesiad from the upper element of *epaxialis*. Anteriorly, *supracarinalis* becomes tendinous, joining its antimere in midline before inserting on supraoccipital crest.

Epaxialis comprises dorsal and ventral segments. Dorsal segment has helically arranged fibres between anterodorsally directed myocommata. Anteriorly segment inserts on posterior area of supraoccipital; medially loosely attached by connective tissue to neural arches and ventrally free from underlying segment. Ventral segment has fibre direction varying from parallel, between posterior myocommata, to anteroventral, between anterior myocommata. Anteriorly, segment trifurcates, upper, principal portion inserts on epioccipital, together with middle portion, lower passes between forked posttemporal limbs to insert on pterotic. Posterior to where middle and lower portions divide, muscle is tendiously attached to tip of cleithrum. Medially, ventral segment is loosely attached to horizontal septum which marks vertebral lateral processes. Laterally, ventral *epaxialis* joins *hypaxialis*. Connection between the muscles effected *via* aponeuroses formed from expansion of ventral margins of anterior (7–8th) epaxial myocommata. Lateral boundary between *epaxialis* and *hypaxialis* marked by wavy course of lateral line nerve.

Hypaxialis single, thin sheet anteriorly comprising seven or eight broad bands of fibres each connected to respective epaxial myocommata (vex, Fig. 25). Anteroventrally, *hypaxialis* attaches to cleithrum, ventromedially to thick, tendinous sheet stretching from pelvic girdle to cleithrum (p. 175). Ventrally, *hypaxialis* joins *infracarinalis anterior*. Postcleithrum runs diagonally across lateral surface of *hypaxialis* to which it is firmly attached. *Lateralis superficialis* (ls, Fig. 25) becomes apparent only at the point where fibres of *epaxialis* and *hypaxialis* become horizontally aligned.

Infracarinalis anterior stretches from medial margin of pelvic bone to symphysial tip of cleithrum. Posteriorly, muscle undifferentiated from *arrector ventralis pelvicus* (see above) and anteriorly from *hypaxialis*. *Infracarinalis medius* is a short segment which immediately passes into the fascia of *hypaxialis*.

COMMENTS. The loose attachments of *epaxialis* segments both medially to the vertebral column and laterally to the *hypaxialis* suggest they are significant functional attributes toward elevating the head. Manipulation of preserved bathygadids show the lower epaxial border capable of sinking below the upper level of the *hypaxialis* and is 'cradled' by the horizontal septum. The position of the lateral line nerve is maintained by its connective tissue adhesion to the *hypaxialis*.

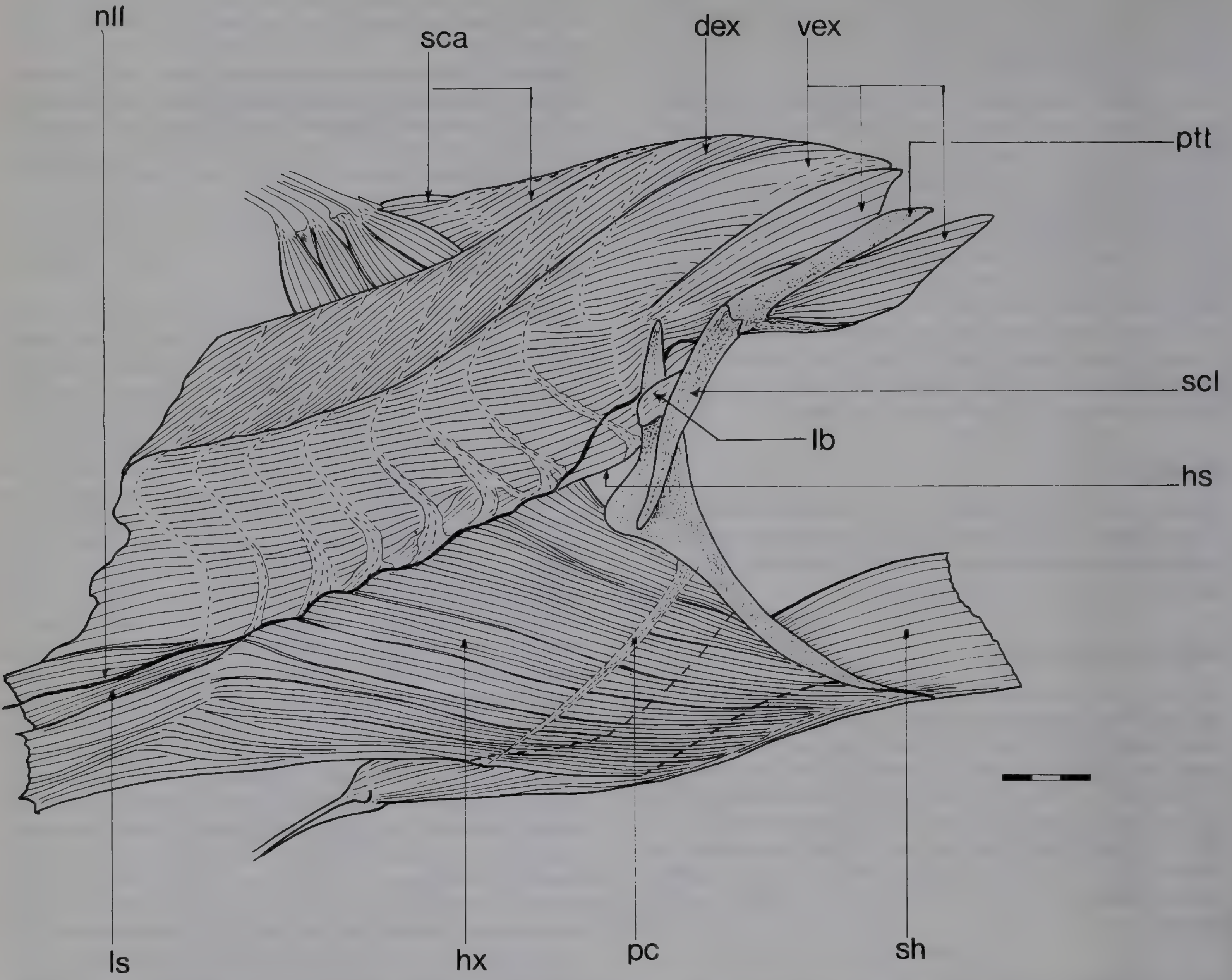

Fig. 25 *Bathygadus favosus*. Anterior body musculature; dashed outline indicates the pelvic-cleithral tendinous sheet; the pectoral girdle and its muscles have been removed.

The tripartite articulation of the cranium with the vertebral column possessed by bathygadids might seem to limit the degree of vertical cranial rotation, but as noted by Rosen & Patterson (1969), the near horizontal arrangement of basioccipital and exoccipital condyles would alleviate such limitation. Although in bathygadids, the exoccipital condyles are reduced in size it appears that the principal factor in achieving cranial elevation is modification of the *epaxialis* which allows greater flexure in the vertical plane. There is striking similarity in anterior body muscle arrangement between bathygadids and stomiatoids, exemplified by *Chauliodus* (Tchernavin, 1953), a fish which also flexes the vertebral column in cranial elevation.

Reduction of epipleural ribs and diminution of regular myotomes in bathygadids also suggests a considerable degree of freedom in anterior body muscle movement, present elsewhere in gadiforms only in Bregmacerotidae.

Pelvic musculature of macrouroids and most gadoids is more extensively developed than in bathygadids and extends well forward to the pectoral girdle where it meets the median septum supporting hypaxial musculature. The entire pelvic girdle of bathygadids is loosely arranged and its tendinous connections with the *sternohyoideus* (in *Gadomus*) and with the *hypaxialis* (see above) supports the idea that a specialized functional sequence is involved in feeding.

We suggest that future attention should be directed toward elucidating the arrangement of anterior body musculature in ‘paracanthopterygian’ fishes. A brief survey of ‘para’ and acanthopterygian taxa suggests that loss of the outer hypaxial layer (*obliquus superioris*) has occurred among ‘paracanthopterygians’.

Ramus lateralis accessorius nerve (RLA)
Fig. 26

The outstanding feature of the RLA in Bathygadidae is the hypertrophy and pathway of its pectoralis branch (RLA-P). The usual gadoid condition (Freihofer, 1970) is for the pectoral branch to diverge from the main vertical pectoral-pelvic trunk (RLA-PP) and loop around the pectoral fin base,

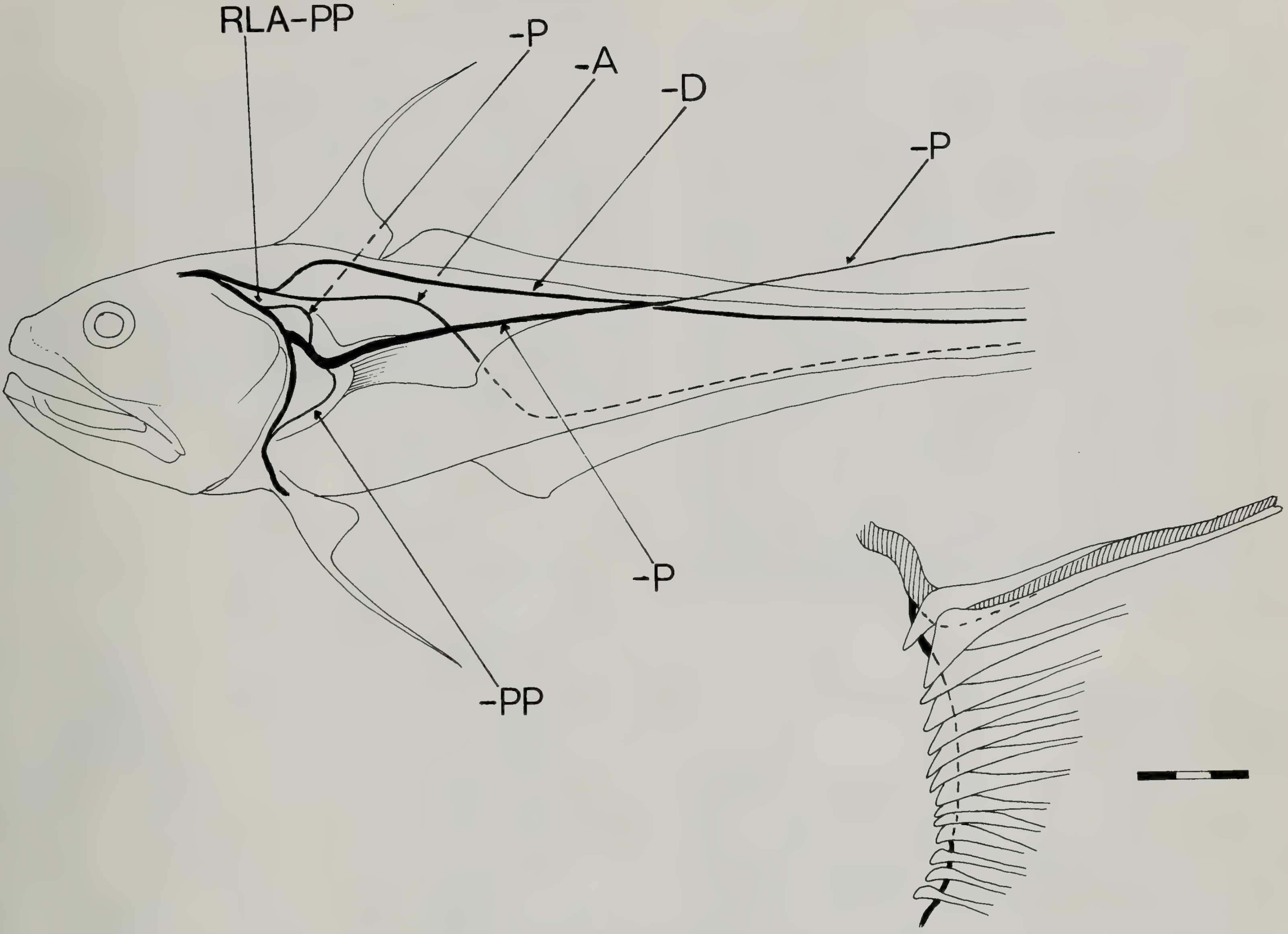

Fig. 26 Pathway of the RLA nerve in a bathygadid (*Gadomus longifilis*, BMNH 1963.2.25:7–17). The pathway of the anal branch has not been detected with certainty, the assumed course is indicated as a dashed line. The enlarged drawing shows in detail the ramification of the pectoral branch, running between the first and second anal fin rays.

with sub-branches of the outer loop innervating fin rays. In *Bathygadus* and *Gadomus* RLA-P branches twice from RLA-PP, first *via* a thin nerve, secondly along the dorsal rim of the pectoral base *via* a thickened branch. The first meets the second some distance before the origin of the 1st fin ray, together they pass between the ray halves, the thickened branch extending between the shortened 1st, and prolonged 2nd rays, eventually lying exposed along outer border of 2nd ray. The first branch passes between bases of fin ray halves, turns caudad and joins main RLA-PP trunk.

Comments. The bathygadid branching pattern, hypertrophy and pectoral ray extension of RLA-P appears unique to that group. Extension of the nerve along 2nd pectoral ray is more pronounced in *Gadomus* since the ray is more attenuated than in *Bathygadus*. Some hypertrophy of RLA-P occurs in Steindachneriidae and it extends slightly between 1st and 2nd pectoral rays. Freihofer (1970, fig. 4) described and illustrated a small branch of RLA-P in *Physiculus* (Moridae). In overall pattern, the anterior ramification of the bathygadid RLA more closely resembles that of Moridae than Gadidae. However, we have been unable to trace fully the connections between the anal fin (RLA-A) and dorsal (RLA-D) branches. The branching pattern of the dorsal ramus (RLA-D) differs, however, from that in both Moridae and Gadidae as illustrated by Freihofer (1970), there being an additional lateral branch diverging from RLA-PP trunk (RLA-L, Fig. 26).

Functional significance of an exposed nerve along the pectoral fin might be that bathygadids extend their pectorals for prey detection. Bardack & Case (1965) recorded how the phycid *Urophycis* samples the environment by extending forward its modified, prolonged pelvic fins and the high degree of sensitivity that these fins have to chemical and mechanical stimulation. Sulak (1977:102) described similar nerve configuration to that of bathygadids in the pectoral fins of the chloropthalmid *Bathypterois*. Here, however, innervation is from the 1st and 3rd spinal nerves; the 1st sends branches along the length of the extended 1st pectoral ray, analogous to the situation in *Gadomus*. Sulak (1977) supposes a 'discriminating sensory role' for the pectoral fins in *Bathypterois*, perhaps capable of sensory stimuli. A similar role is hypothesised for the elongated bathygadid pectoral fins. Of interest is Freihofer's (1970) observation of hypertrophy and exposure of RLA-D serving the 1st dorsal fin spine in the macrouroid *Lionurus*.

JUVENILE BATHYGADIDS

Only one pelagic juvenile bathygadid has been recorded previously (Fahay & Markle, 1984:267) of *ca* 30mm TL, identified as *Gadomus*. Three others are recorded here identified as *Bathygadus*. sp. (USMN 288422), 68.5, 70.5 and 74mm TL, head lengths are, respectively, 12, 12 and 12.7mm; pectoral fin rays 15–16, pelvic rays 8, fin rays of both pectoral and pelvics filamentous, those of dorsal fins too damaged to ascertain their filamentous nature. Gill-rakers 2(n1)–3(n2) + 10. Mental barbel lacking. Guts distended and full of calanid copepods (Euchaetidae, including *Euchaeta spinosa* and Augaptilidae). Specimens were recovered from stomach of an *Alepisaurus ferox* from Gulf of Mexico (30° 28′S, 89° 31W; 24.11.1966). The species to which these juveniles belong is uncertain as they exhibit no characters diagnostic for adults (Merrett, 1986). It is assumed that gill-raker number increases throughout growth. At these stages, denticles, found on rakers of adults are lacking.

MODE OF LIFE
(Fig. 1)

Marshall (1979:276) noted that swimming action of bathygadids is unlike that of macrouroids which swim nose-down and undulating tail up. Bathygadids, on the contrary, swim steadily, parallel to the sea-floor (Marshall & Bourne, 1964). Differences in swimming modes are due to the reverse pattern of dorsal and anal fin enlargement, in bathygadids, the dorsal rays being longer than the anal and so making for a headlifting, tail down mode.

The food of bathygadids, *viz*. copepods, amphipods, euphausiids, mysids and decapods, suggests the fish chase moving prey (Marshall, 1979). The large, pectoral RLA nerve exposed along the outer extended pectoral ray indicates a high sensitivity of the fin-rays to external movement. Perhaps, like some bathypteroids, the rays contain gustatory cells that enable distant detection of prey (p. 183). Bathygadids possibly maintain a near stationary level above the substrate, punctuated by rapid prey-capture swimming sequences. Rapid flexure of body musculature probably elevates the head during prey-capture (p. 181). The photograph of what appears to be *Bathygadus furvescens* in Marshall & Bourne (1964, pl. 2) clearly demonstrates the lateral attitude of pectoral and pelvic fins as the fish maintains position in the water column and undoubtedly pursues a somewhat leisurely swimming action, as do other gadoids (eg. *Gadus*).

The short gill-filaments of bathygadids suggest they live either in well-oxygenated water or they expend little energy. Their depth range suggests they encounter oxygen-poor levels and it is more likely they have a low VO2 achieved by reduced activity. Their thin scales suggest oxygen exchange across the skin may even occur.

HOMOPLASY BETWEEN GADIFORMS AND OPHIDIIFORMS

During the course of out-group comparisons, we were struck by the similarity of the ophidiiform neobythitine *Lamprogrammus nigricans* to bathygadid species. This taxon shares with *Bathygadus* and *Gadomus* five supposedly derived characters, namely: 1) body scales with reticulate pattern of circular and transverse ridges, 2) wide separation between premaxillary dentigerous areas, 3) reduced gill-filaments, those on 1st arch less than half the length of outer gill-rakers, 4) broad nasal bones, in midline contact posteriorly and separated anteriorly by rostral cartilage (shared with *Bathygadus*), 5) narrow and elongate interoperculum with dorsally humped margin (shared with some *Bathygadus* species; Fig. 17).

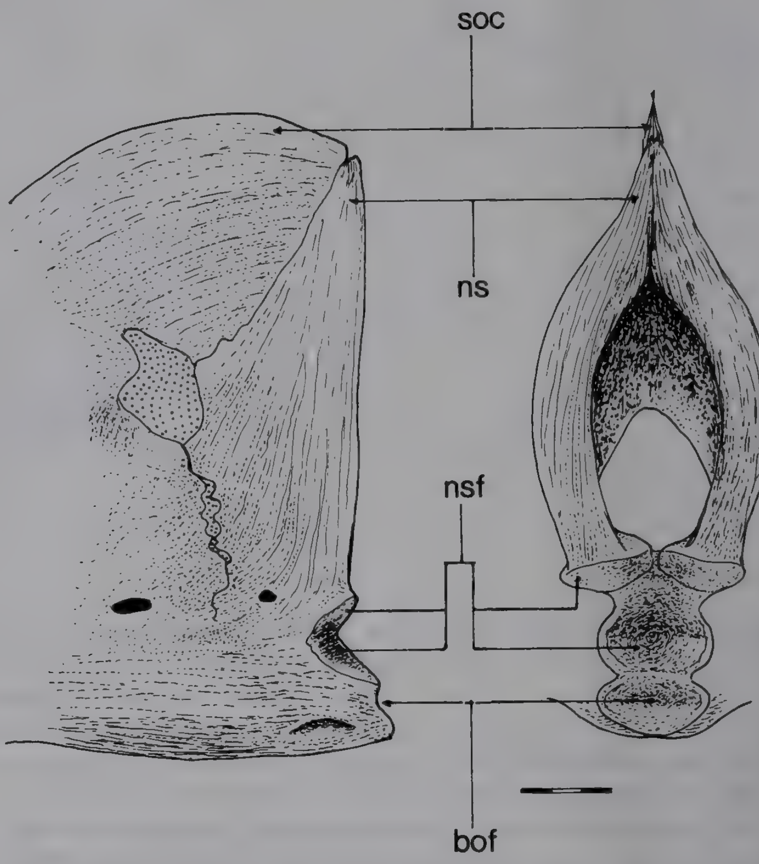

Fig. 27 *Lamprogrammus nigricans* (BMNH 1939.5.26:1483–7). Posterior region of the cranium in lateral and posterior views to show fused neural spine.

In contrast to bathygadids, *Lamprogrammus nigricans* possesses a trigemino-facialis foramen in the lateral face of the braincase, a feature lacking in Gadiformes and one synapomorphic for that group (Howes, 1989). In view of the number of homologies shared with bathygadids, the presence of a trigemino-facialis chamber might be regarded as secondarily derived in *Lamprogrammus*. This assumption is anatomically unsound, however, since to 'regain' this feature would require associated reorganization of attendant nerves and vessels and it is more parsimonious to assume that the 'synapomorphies' are homoplasies.

Lamprogrammus has a strong ligament connecting the inter-operculum and hyomandibular, a feature found in other bythitoid ophidiiforms examined. Previously considered synapomorphic for gadoids (Howes, 1988; 1989) one must now consider the possibility that its presence might indicate sister-group relationship of at least some 'ophidiiforms' with gadiforms. Alternatively, accepting Patterson & Rosen's (1989) revised view of paracanthopterygian relationships, the ligamentous connections would be viewed as lost in batrachoidiforms, lophiiforms and macrouroids.

In common with other *Lamprogrammus* species, *L. nigricans* possesses vomerine and palatine teeth, both are absent in bathygadids (p. 162). *Lamprogrammus* has a sensory canal running along the dorsum of the body. The canal comprises *ca* 30 evenly-spaced neuromasts each mounted on a large scales, covered laterally by a hemitube of scale-bearing skin. The canal is not a lateral line canal as previously reported by Cohen & Nielsen (1978:34) but a dorsal branch of nerve RLA-D (p. 183); the lateral line nerve follows the more usual course along the midlateral line of body.

It is noted that the posterior cranial region of *Lamprogrammus* shows evidence of occipital fusion with the 1st (or an accessory) vertebra (Fig. 27). In *L. nigricans* there is a marked posterior suture between the supraoccipital crest and vertical lamella of what is apparently a neural arch. Anteriorly a large area of cartilage separates the 'neural arch' from the supraoccipital and a synchondrosis extends ventrally from this area to disappear in the exoccipital region. Situated posteriorly to the ventral margin of the suture is the 1st spinal nerve foramen which indicates the basal region of the fused neural arch. The posterior lateral cranial facets are elliptical and ventrally directed, the medial facet is double, the upper circular with a steep downward slope, the lower oblate and vertical. A similar arrangement of facets is illustrated by Rosen & Patterson (1969, fig. 10E) for the bythitoid *Dinematichthys*, a morphology which also occurs in *Genypterus*, *Brotula* and *Neobythites*. The lateral and upper medial facets possibly represent those of the fused neural arch and the lower, vertical facet that of the basioccipital.

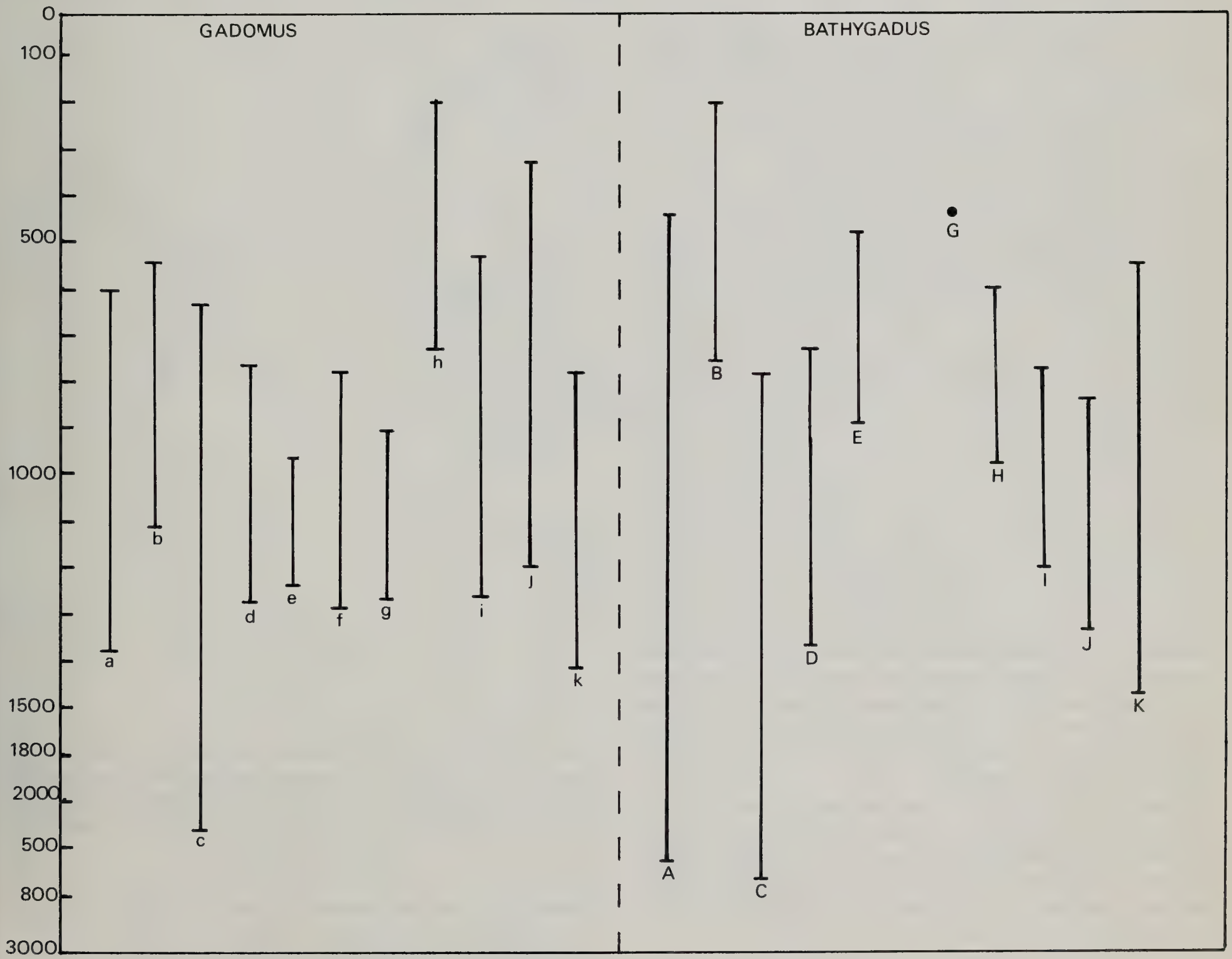

Fig. 28 Depth distribution (in metres) of *Gadomus* and *Bathygadus*. *Gadomus* species are indicated as; a=*arcuatus*, b=*dispar*, c=*longifilis*, d= *multifilis*, e=*aoteanus*, f=*furvescens*, g=*magnifilis*, h=*denticulatus*, i=*introniger*, j=*colletti*, k=*melanopterus*. *Bathygadus* species are indicated as; A= *melanobranchus*, B=*macrops*, C=*favosus*, D=*cottoides*, E=*spongiceps*, G=*entomelas* (type only), H=*sulcatus*, I=*antrodes*, J=*nipponicus*, K=*bowersi*.

TAXONOMY

BATHYGADIDAE

Bathygadinae Jordan & Evermann, 1898:2562.

Diagnosis. Family of gadoid fishes distinguished from others in: specialised nature of anterior body musculature, where *infracarinalis anterior* well-separated from *hypaxialis* and markedly tendinous; in modified nerve pathway of *ramus lateralis accessorius* serving pectoral fin, where branch supplying first and second ray is hypertrophied and extends along second ray; in reduced gill-filaments which are (with one exception) always less than half the length of the gill-rakers, and in absence of caudal fin skeleton.

Included genera: *Bathygadus* Günther, 1878
Gadomus Regan, 1903

In the following species accounts, only principal taxonomic references listed in synonymies.

Bathygadus Günther, 1878

Bathygadus Günther, 1878:23 (type, *B. cottoides* Günther, 1878 by monotypy).
Melanobranchus Regan, 1903:459 (type, *Bathygadus melanobranchus* Vaillant, 1888 by original designation).
Regania Jordan & Gilbert 1904:602; 604 (type *R. nipponicus* Jordan & Gilbert, 1904 by original designation).

Diagnosis. (Features distinguishing *Bathygadus* from *Gadomus* are italicised). Head and body compressed, tail slender, without caudal fin; two dorsal fins, the first with two spiny rays, first ray reduced. Rays of second dorsal fin longer than those of anal fin. *Dorsal, pectoral and pelvic rays rarely attenuated and if so, not extending beyond centre of body.* Snout blunt, mouth large and terminal; *teeth minute to moderate* in size, villiform; *dentigerous areas of premaxillae usually widely separated across midline. Palatine contacts lateral ethmoid and mesethmoid. Barbel rarely present and when so, minute and often concealed beneath skin. Interoperculum variable in shape, but shallow and sometimes crook-shaped, with angular posterior border; not visible below border of preoperculum.* Gill-opening wide; gill-rakers on first arch slender and denticulate; gill-filaments reduced, at most 25% length of rakers (except in one species); pseudobranch present. *Nasal bones broad and may be narrowly separated, or even meet, posteriorly, in the midline.* Skull with generally broad interorbital width, rarely <25% of head length, orbit often >25% of head length. *Number of vertebrae < 100.* Scales small, bearing fine reticulate pattern. *Olfactory bulbs midway between olfactory lobes of brain and the nasal cavity. Two retia in swimbladder.*

Gilbert & Hubbs (1920) and subsequent authors are followed in recognising *Melanobranchus* and *Regania* as synonyms of *Bathygadus*. Weber & de Beaufort (1929) considered *Bathygadus* as comprising the subgenera *Bathygadus* and *Gadomus*. The present anatomical findings point to a more distinct dichotomy.

Atlantic species

Adequate keys to Atlantic Ocean species of *Bathygadus* have been produced by Iwamoto (1970) and Marshall (1973*a*). The following are additional data and comments on the three species.

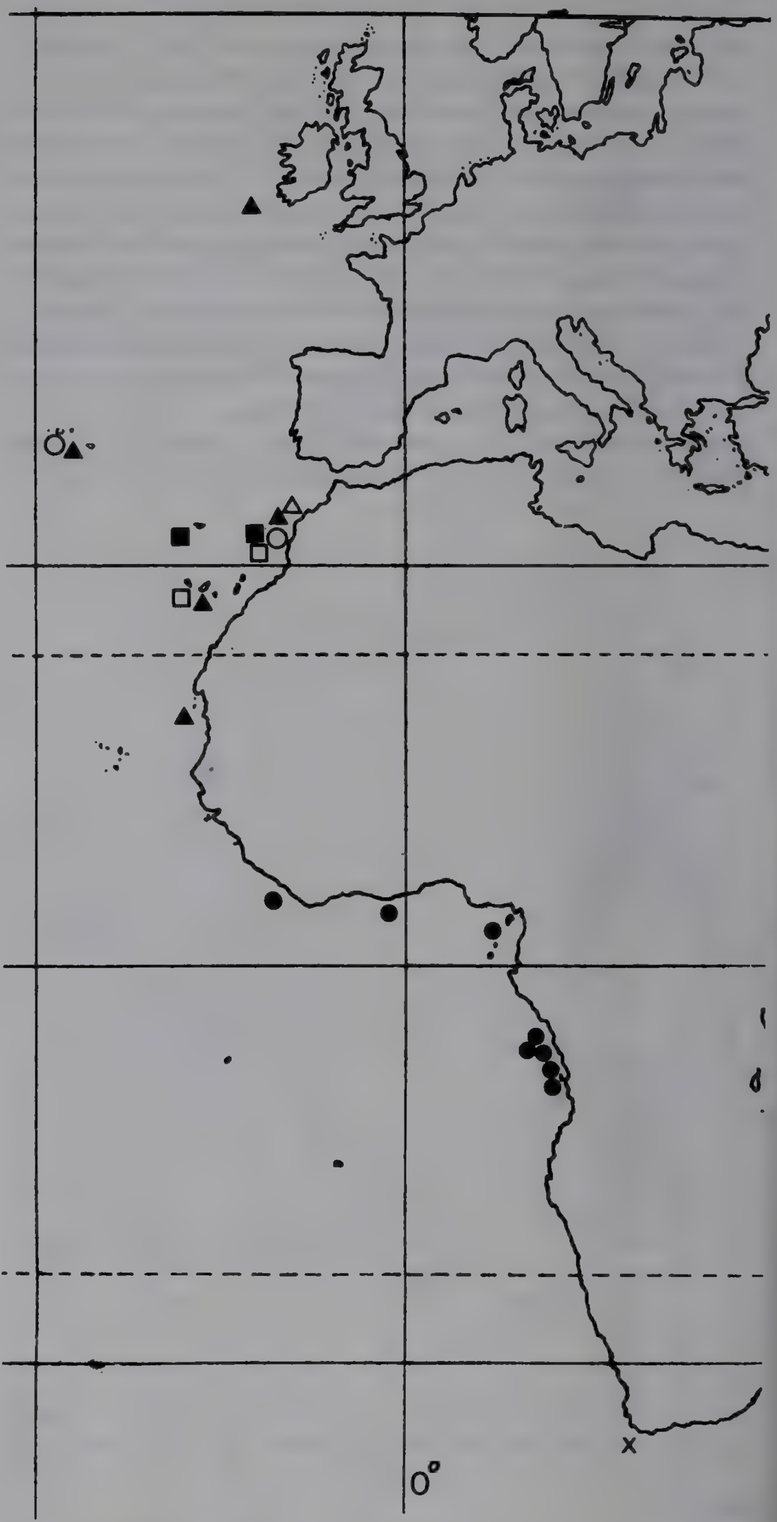

Fig. 29 Eastern Atlantic distribution of *Bathygadus* and *Gadomus* species. ■=*B. favosus*, ▲=*B. melanobranchus*, ●=*B. macrops*, 0=*G. longifilis*, △=*G. dispar*, X=*G. capensis*. Records mainly from Poll (1953) and Marshall (1973*a*). Each symbol may represent more than one collecting station.

Bathygadus melanobranchus Vaillant, 1888

Bathygadus melanobranchus Vaillant, 1888:206 (description).
Melanobranchus melanobranchus; Regan, 1903:459.
Bathygadus vaillanti Roule & Angel, 1933:63.

Iwamoto (1970) and Marshall (1973*a*) give complete synonymies and Marshall (1973*b*) gives additional references.

Iwamoto (1986:332) comments on southern African records and Arai (1983) provides descriptions of Surinam-shelf specimens.

Marshall (1973*a*) distinguished *B. melanobranchus* from *B. macrops* not only on interorbital width and absence of barbel (see under *B. macrops*) but also on darkly pigmented gill-filaments of the first arch. Although preservation tends to obscure this feature, pigmentation is present in all the specimens examined in this study. The number of gill-rakers in *melanobranchus* is mostly higher than in other Atlantic species, being 21–24, *cf.* 18–22, such a high number is present only in the Indo-Pacific species *B. antrodes* and *B. bowersi*.

As noted by Marshall (1973*a*), specimens examined show an allometric relationship between head length and interorbital width, the latter decreasing with increasing head length. In relation to increasing body length, however, head length remains proportionately constant. All our proportional measurements are within the ranges given for those parameters by Iwamoto (1970) and Marshall (1973*a*).

The assumption by Iwamoto (1970:342) that *melanobranchus* is closely related to *B. nipponicus*, *entomelas* and *furvescens* is unsupported by any revealed synapomorphies, although we agree that *melanobranchus* does not closely resemble the other two Atlantic species.

DISTRIBUTION. Western and eastern Atlantic and mid-Atlantic ridge (off Azores), ? south to the Cape, South Africa. According to Iwamoto (1986:332) the specimens on which South African records of this species have been based cannot be traced, neither have we been successful in locating this material and thus this extension of the species' range cannot be verified (but see p. 195).

DEPTH RANGE. 450–2560m (Marshall, 1973*a*). Merrett & Marshall (1981) found *B. melanobranchus* to be one of the most numerous species of fishes collected off north-west Africa, occupying a depth range of 734–1017m.

MATERIAL EXAMINED. BMNH 1890.6.16:35–6, (syntypes) off Arguin Bank, Mauritania; 1934.12.19:26–7, 96.0, 99.8mm s-a, 37° 37′N, 25° 20′W; 1963.2.25:31–35, 131–150mm s-a, 'Oregon' Stn 3586; USNM 202777, off Zaire coast; Uncat. 147mm s-a, off Panama. USNM 74342 (from paratype series of *B. favosus*; see p. 189), NE Gulf of Mexico, 'Albatross' Stn 2394.

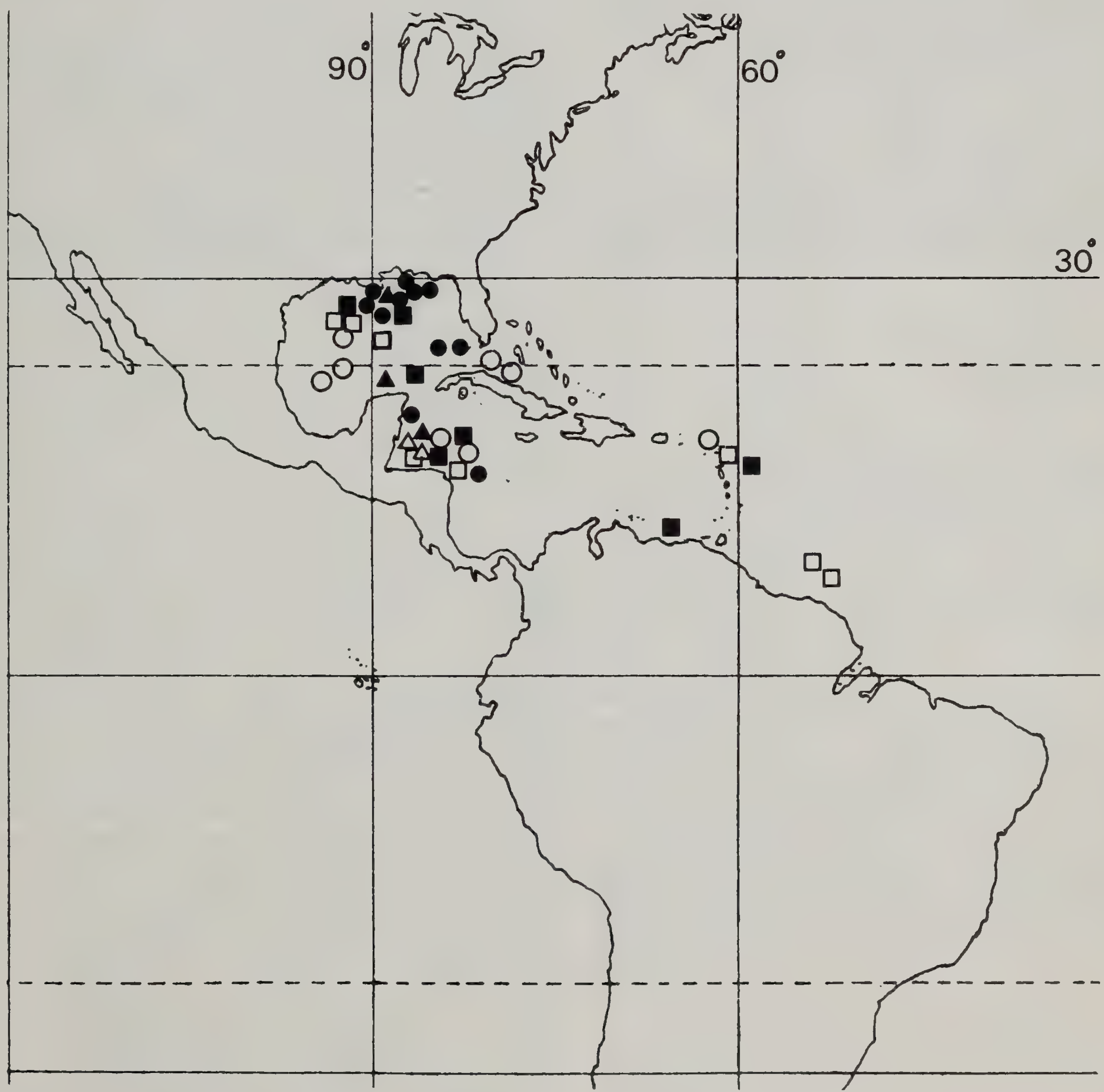

Fig. 30 Western Atlantic distribution of *Bathygadus* and *Gadomus* species. Symbols as in previous figure. Records from Iwamoto (1970), Marshall (1973*a*) and Arai (1983). Each symbol may represent more than one collecting station.

Bathygadus macrops Goode & Bean, 1885

Bathygadus macrops Goode & Bean, 1885:598.
Bathygadus goethemi Poll, 1953:219.

Iwamoto (1970) and Marshall (1973*a*) give complete synonymies and Iwamoto (1986:331) provides descriptions of South African forms.

Bathygadus macrops distinguished from other Atlantic species by presence of small barbel, narrower interorbital width (18.0–27.0% of head length, *cf.* 24.1–39.0%), and from other species by length of gill-filaments which equal or exceed that of gill-rakers. Size of eye distinguishes *macrops* from *favosus* (26.0–34.0% of head length, *cf.* 19.0–24.0%) but not from *melanobranchus* (24.7–34.2% of head length). Teeth arranged in definite parallel rows on premaxilla. Only a single tooth band on dentary. Second pectoral ray somewhat filamentous, at least in juveniles.

Pyloric caeca could be counted in only two specimens of 94 and 100mm s-a length and number, respectively, 22 and 40. Three specimens of 106, 111 and 128mm s-a length possess ripe testes.

According to Marshall (1973*a*) *B. macrops* is most closely related to *B. sulcatus* of the Philippine Islands but differs in having fewer pelvic rays (8, *cf.* 9–10), larger eyes and shorter snout. Such differences occur between *macrops* and other species and we can find no evidence to support such a close relationship.

DISTRIBUTION. Western and eastern Atlantic.

DEPTH RANGE. 200–770m (Marshall, 1973*a*).

MATERIAL EXAMINED. USNM 37339 (Holotype), 103mm s-a; 53047 (Paratypes) 70, 74mm s-a, 28° 34′N, 86° 48′W; USNM (un-numbered), 80, 96, 106, 111, 126, 134, 145mm s-a, 03° 65′S, 09° 15′E; BMNH 1973.3.5:3–6, 73.5, 81.5, 86mm s-a, 9° 10′N, 15° 99′W.

Bathygadus favosus Goode & Bean, 1885

Bathygadus favosus Goode & Bean, 1885:160.

Iwamoto (1970) and Marshall (1973*a*) give complete synonymies; Marshall (1973*b*) gives additional references and Iwamoto (1986:331) provides descriptions of South African forms.

Bathygadus favosus distinguished from other Atlantic species by higher number of pelvic fin rays, *viz.* 9 (rarely 10) *vs* 7–8 in others, and broader interorbital width (29.6–39.4% of head length, *cf.* 24.1–27%). As in *B. melanobranchus*, a barbel is lacking. Pyloric caeca were counted in only four specimens but fewer in number than in the other two species; counts are 15(150), 15(91), 16(60), 23(113) (numbers in parentheses refer to the s-a length in mm).

Marshall (1973*a*) related *B. favosus* to the broad-headed species of the Philippine-Indonesian area. Elsewhere (p. 200) we indicate that there is a continuum of cranial width in *Bathygadus* and on this basis alone we are unable to support Marshall's contention.

DISTRIBUTION. Given as western and eastern Atlantic by Marshall (1973a, *b*), but recorded from the mid-Atlantic Ridge by Pakhurov (1980).

DEPTH RANGE. 770–2745m.

MATERIAL EXAMINED. USNM 74342 (Paratypes) 156, 146mm s-a, and four others too damaged to measure (the two

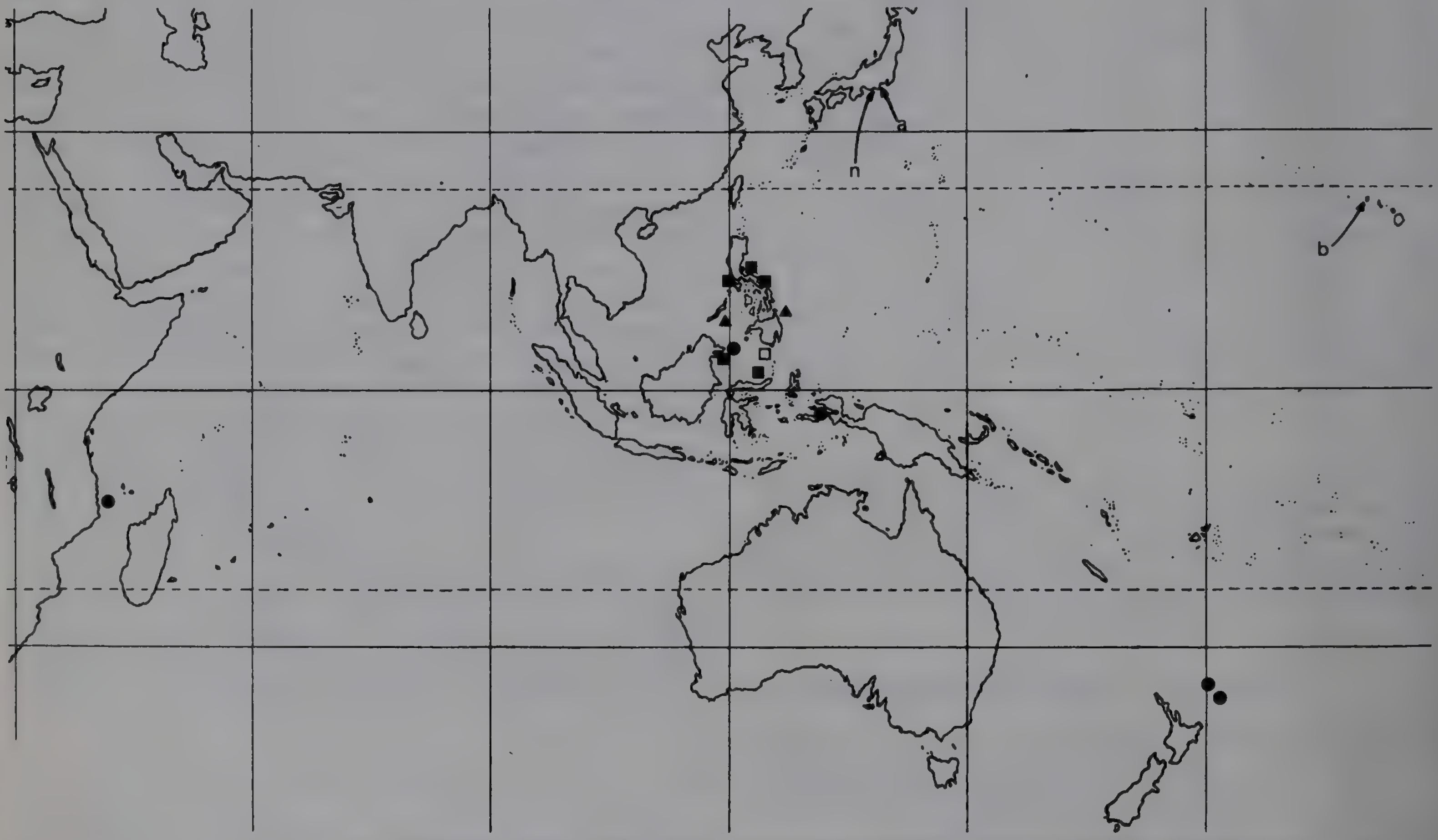

Fig. 31 Indo-Pacific distribution of *Bathygadus* species. □=*B. entomelas*, ■=*B. spongiceps*, ●=*B. cottoides*, ▲=*B. sulcatus*, a=*B. antrodes*, n=*B. nipponicus*, b=*B. bowersi* (Hawaii).

smallest specimens in this lot are re-determined as *B. melanobranchus*), NE Gulf of Mexico 'Albatross' Stn 2394; 34918, 34910 (Paratypes) 113, 157mm s-a, Lesser Antilles; BMNH 1903.2.25.20–25, 116.5mm s-a, off Panama 'Oregon' Stn 3586.

Indo-pacific species

Bathygadus cottoides Günther, 1878

Bathygadus cottoides Günther, 1878:23 (brief descr.); 1887: 154 (detailed descr.).
Regania filamentosa Smith & Radcliffe, 1912:149 (listed).
Bathygadus melanobranchus; Weber, 1913 (*non* Vaillant):172 (descr.).
Bathygadus dubiosus Weber, 1913:173 (descr.).
Bathygadus filamentosus; Gilbert & Hubbs, 1916:149 (listed).
Bathygadus filamentosus; Gilbert & Hubbs, 1920:384 (descr.).
Bathygadus furvescens: Gilbert & Hubbs, 1920 (*non* Alcock): 388 (Philippines).
Bathygadus (Gadomus) filamentosus; Weber & de Beaufort, 1929:16 (synonymy; descr.).
?*Bathygadus spongiceps*; Norman, 1939 (*non* Gilbert & Hubbs): 48 (descr.).
?*Bathygadus* sp. Iwamoto, 1986:93 (descr.).

Described by Günther from fourteen specimens, all apparently in poor condition. There are now six syntypes in the BMNH, from five of which we have made our measurements (one specimen being too badly damaged to include). In all but one specimen the pectoral fins are broken off at their bases so that it is impossible to count the rays. In the exceptional specimen only the bases of the rays remain. Günther records 10 pectoral rays for the species, but we count 14 in this specimen. We also count II, 6–7 dorsal rays, whereas Günther gives a total of 8, presumably having overlooked the first, reduced ray.

Gilbert & Hubbs (1920) synonymised *B. dubiosus* Weber, 1913 with *B. filamentosus*. An examination of the holotypes of these species reveals almost identical morphometric and meristic features (Table 3). The present study revealed no morphometric, meristic or other differences that distinguish *B. filamentosus* from *B. cottoides* and so those species are treated as synonymous.

The specimens described by Gilbert & Hubbs (1920:388) as *B. furvescens* Alcock, 1894 are certainly not that species and are possibly *B. cottoides*. Only one of their specimens was located (USNM 99450 from between Siquijor and Bohol Island, Philippines) and a close correlation between all parameters was found (Table 2).

Norman (1939) reported a specimen, possibly of *B. spongiceps*, from the Zanzibar area: This appears to be close to, if not conspecific with *B. cottoides*. The Zanzibar specimen matches *B. cottoides* in almost every respect with the exception of having 9 instead of 8 pelvic rays, a shorter head (50.7 *cf.* 52.9–57.6% of s-a length) and a broader interorbital width. The midline premaxillary tooth-patch separation is narrower, being 11.6 of the premaxillary length, *cf.* 14.2–20.0% in *B. cottoides*. This specimen also closely resembles the *Bathygadus* sp. recorded by Iwamoto (1986) except that Iwamoto records 9–12 pyloric caeca whereas in the Zanzibar specimen there are 23.

McCann & McKnight (1980) recorded *B. cottoides* from the eastern New Zealand slope, but measurements they give differ from ours in several respects. There are fewer pectoral and pelvic fin rays, fewer gill-rakers, a longer head and shorter upper jaws in their specimens (see Table 2). We are unable to say whether their specimens are *B. cottoides*, the differences in proportions may merely reflect the larger size of their specimens.

Table 2 Counts and proportional measurements for six syntypes of *Bathygadus cottoides*, a specimen from near Zanzibar and a specimen from New Zealand (data taken from McCann & McKnight, 1980).

	Syntypes	Mean	Zanzibar spec.	From McCann & McKnight, 1980.
D	II6–8		II7	II6
Pe	14–15		15	10–11
Pl	9		9	8
GR	5–6+18–22		6+20	5+15
PC	?		23	?
s-a	26.0–63.3mm		97.5mm	102mm
bd	35.3–48.1	40.4	45.1	46.0
pl	broken		broken	14.7
hl	52.9–57.6	55.1	50.7	60.7
od	16.7–20.8	19.0	24.2	20.9
io	26.8–33.8	30.7	40.3	35.4
pml	56.4–61.5	58.5	60.6	53.2
pma	22.8–26.8	24.9	24.0	?
pms	14.2–20.0	16.8	11.6	?

Table 3 Counts and proportional measurements for the holotype and paratype of *Bathygadus filamentosus* and for the holotype of *Bathygadus dubiosus* (considered synonyms of *B. cottoides*).

	Holotype	Paratype	*B. dubiosus*
D	II8	II8	II8
Pe	13	14	14
Pl	8	8	8
GR	6+20	6+20	6+19
PC	12	?	?
s-a	73mm	54mm	80mm
bd	43.1	42.5	42.5
pl	50.0	broken	77.5
hl	57.5	55.5	56.2
od	23.8	20.0	24.4
io	36.1	31.3	35.5
pml	59.9	61.6	56.6
pma	22.0	16.2	23.5
pms	12.0	7.0	9.7

DISTRIBUTION. Off Kermadec Islands, Indonesia (? and east coast of Africa).

DEPTH RANGE. 700–1400m.

MATERIAL EXAMINED. BMNH 1887.12.7.139 (Syntype) 56.5mm s-a, N.E. of New Zealand: 1887.12.7:140–3 (Syntypes) 63.3–33m s-a; 144–5 (Syntypes), 26mm s-a, all from near Kermadec Islands; 1939.5.24:677, 97.5mm s-a, Zanzibar area; USNM 72924 (Holotype of *B. filamentosus*), 73mm s-a, near Sipadan Island, east coast of Borneo; 148990 (Paratype of *B. filamentosus*), 54mm s-a, Molucca Passage; ZMA 114.896 (Holotype of *B. dubiosus*), 80mm s-a, 03° 37'S, 131° 26'E.

Bathygadus spongiceps Gilbert & Hubbs, 1920

Bathygadus spongiceps Gilbert & Hubbs, 1920:381 (descr.).

Known from the types (seven specimens).

In their key, Gilbert & Hubbs (1920) separate *B. spongiceps* from *B. cottoides* on the number of gill-rakers (6+19–22, *cf.* 6+17) and on the larger diameter of the eye of the former. In fact, the gill-raker count for *B. cottoides* is 5–6+18–22 *cf.* 5–6+19–22 in *B. spongiceps*, and the orbital diameters (measured as percentages of the head lengths in both species), almost completely overlap. The interopercular shapes of the two species are also virtually identical (Fig. 17, *cf.* 1 & 8). Only in the upper jaw is there a marked discrepancy between the species; the length of the premaxilla in *B. cottoides* is 56.4–61.5% of the head length, while that of *B. spongiceps* is 52.3–55.0%; the height of the ascending process is greater in the latter species, *viz.* 26.1–31.6% *cf.* 22.8–26.8% of the premaxillary length. There is also a greater midline separation of the premaxillary dentigerous surfaces in *B. cottoides*: 14.2–20.0% *cf.* 7.6–12.9% of the premaxillary length. In *B. spongiceps* there are 15–16 pectoral fin rays, *cf.* 12–15 in *B. cottoides*.

These differences may simply represent clinal variation within a single species. However, without the benefit of material from intermediate geographical areas *B. spongiceps* is here regarded as specifically distinct from *B. cottoides*.

Counts and measurements for the holotype and three paratypes (four others are too poorly preserved to make accurate measurements) are given in Table 4.

Table 4 Counts and proportional measurements for the types of *Bathygadus spongiceps* and *B. entomelas*

	spongiceps holotype	*spongiceps* paratypes (3)	*entomelas* holotype
D	II9	II8	II8
Pe	16	15	16
Pl	9	9	10
GR	6+22	5–6+19	5+21
PC	?	6 & 12	37*
s-a	115mm	73, 94, 97mm	87mm
bd	40.0	41.2–45.2	41.3
pl	24.0	27.0 (1 spec.)	broken
hl	51.3	51.5–58.9	55.0
od	20.6	17.4–21.6	27.0
io	36.4	25.5; 30.9; 40.0	32.2
pml	52.5	52.3–55.0	48.9
pma	27.4	26.1–31.6	23.4
pms	12.9	7.6, 11.0	10.6

* 35, according to Gilbert & Hubbs, 1920.

DISTRIBUTION. China and Celebes Seas.

DEPTH RANGE. 864–1600m.

MATERIAL EXAMINED. USNM 78210 (Holotype), 115mm s-a, Derval Bay, Borneo, northeastern coast; USNM 220978 (paratype), 73mm s-a, off south Luzon, China Sea; USNM 220979 (paratype), 94mm s-a, North Island, Celebes; USNM 078235 (paratype), 97mm s-a, Atulayan Island, Philippines (13° 35′N, 123° 37′E). Three other paratypes, USNM 220980 from the southeast coast of Luzon are too badly damaged to derive any accurate measurements and counts.

Bathygadus entomelas Gilbert & Hubbs, 1920

Bathygadus entomelas Gilbert & Hubbs, 1920:386 (descr.).
Bathygadus (Bathygadus) entomelas; Weber & de Beaufort, 1929:18 (descr. after Gilbert & Hubbs).

The species is known only from the type specimen collected in the Molucca Passage. It strongly resembles specimens of *B. spongiceps* and was distinguished from that species by Gilbert & Hubbs (1920) on the basis of its larger orbit. *Bathygadus entomelas* also differs from *B. spongiceps* (and other species) in possessing 10 pelvic fin rays and a large number of pyloric caeca (37, *cf.* 6–12). In its dentition and overall morphology, *entomelas* most closely resembles *B. spongiceps*.

In their key, Gilbert & Hubbs (1920) separated *B. entomelas* from *B. sulcatus* in the supposed absence of a barbel. However, like *sulcatus*, *B. entomelas* has a minute barbel hidden beneath the skin at the lower jaw symphysis.

B. entomelas night be recognised as a synonym of *B. spongiceps* if those differences that do exist are regarded as intraspecific variability. However, in view of the lack of specimens it is impracticable to assess such variability and so the species is here retained.

DISTRIBUTION. Philippines.

DEPTH RANGE. 780m.

MATERIAL EXAMINED. USNM 78211 (Holotype and only known specimen), 87mm s-a, Molucca Passage, Philippines. Meristic and morphometric data are given in Table 4.

Bathygadus sulcatus (Smith & Radcliffe, 1912)

Regania sulcata Smith & Radcliffe, 1912:108 (descr.).
Bathygadus sulcatus; Gilbert & Hubbs, 1916:142 (listed).
Bathygadus sulcatus; Gilbert & Hubbs, 1920:390 (descr.).

Smith & Radcliffe (1912) noted the close resemblance of *B. sulcatus* to *B. nipponicus*, but distinguished their species by its higher arched dorsal profile, narrower interorbital width and larger eye. Certainly, *B. sulcatus* has a deeper body than *B. nipponicus*, but is is no deeper than that of the types of *B. garretti*, which name we consider to be synonymous with *B. nipponicus*. In its interorbital width, however, *B. sulcatus* does differ, both from *B. nipponicus* and *B. garretti*, the range being below that of other Indo-Pacific species. *viz.* 23.5–26.4, *cf.* 26.8–37.5% of head length. The diameter of the orbit, although only slightly greater than that of the type

Table 5 Counts and proportional measurements for *Bathygadus sulcatus*. Data from the holotype are included in the Mean.

	Holotype	4 other specimens (USNM149276–82, 192598)	Mean
D	II9	II9–10	
Pe	17*	16–17	
Pl	10**	9–10	
GR	5+18	6+17–18	
PC	30	?	
s-a	161mm	49.0–176.5mm	
bd	41.6	36.0–42.1	39.0
pl	37.2	24.4–30.7	30.7
hl	52.1	50.5–57.1	54.1
od	27.9	26.9–29.8	28.9
io	23.8	23.5–26.4	25.2
pml	57.7	49.6–57.1	55.5
pma	20.6	21.8–26.0	23.2
pms	10.3	4.7–9.5	8.0
bl	concealed	0.2 (1 measured)	

* given as 16 by Smith & Radcliffe (1912)
** given as 9 by Smith & Radcliffe (1912)

of *B. nipponicus*, is embraced by that of the two types of *B. garretti*. Smith & Radcliffe (1912) note the interpremaxillary symphysial space as being 75% of the diameter of the pupil. Although the maximum premaxillary separation in *B. sulcatus* is 10.3% of the premaxillary length, there is a wide variation in the five specimens measured (see Table 5).

Gilbert & Hubbs (1920:391) consider the interoperculum to differ in shape from that of other Philippine species in that its posterior half, and posterior border are almost straight. The present study reveals that in common with other *Bathygadus* species, the posterior margin of the bone is rounded (Fig. 17, 5). Like *B. nipponicus* (the types of *B. garretti*) a minute barbel is concealed beneath the skin at the mandibular symphysis. Only in one specimen is it exposed and it measures 0.6mm.

Although there is apparently only one major morphometric difference between *B. sulcatus* and *B. nipponicus*, *viz*. the width of the interorbital space, *B. sulcatus* is nonetheless regarded here as a separate species. This is simply because the presently recognised distribution of the two taxa is allopatric, but the Japanese and Philippine 'species' might well exhibit a population difference within a more widely distributed species.

DISTRIBUTION. Sulu sea, Philippines.

DEPTH RANGE. 600–954m.

MATERIAL EXAMINED. ISNM 72925 (Holotype), 161mm s-a, Cagayan Island, Sulu Sea, 9° 37′ 35″N, 121° 12′ 37″E; USNM 192598, 176.5mm s-a, from near Cagayan Island; USNM 149176–82, 49, 57, 75mm s-a, off northern Mindanao; between Marinduque and Luzon; between Siquigor and Bohol, and near Cagayan Island. Although noted as paratypes in the USNM collection, none was designated in the original description, nor subsequently by Gilbert & Hubbs (1920). There is no evidence to suggest that these specimens were used in compiling the original description which appears to be based solely on the holotype.

Bathygadus antrodes (Jordan & Gilbert, 1904)

Melanobranchus antrodes Jordan & Gilbert (1902) 1904:606 (descr.).
Bathygadus antrodes; Gilbert & Hubbs, 1916:149 (descr.).
Bathygadus antrodes; Okamura, 1970a:30 (descr.).

Table 6 Counts and proportional measurements for *Bathygadus antrodes*. Data from the holotype are included in the Mean.

	Holotype	8 other specimens (see material examined)	Mean
D	II8	II8	
Pe	13	12–15	
Pl	9	8	
GR	6+21	5–7+20–24	
PC	?	10, 13, 14 & 15	
s-a	95mm	65–129mm	
bd	41.0	38.5–54.8	42.7
pl	broken	26.3–41.2	30.3
hl	55.2	51.8–58.4	54.3
od	22.8	19.8–23.4	21.6
io	32.3	32.2–37.1	34.4
plm	53.3	51.4–55.9	53.3
pma	23.2	23.6–26.5	24.8
pms	14.6	10.0–12.5	10.2

Bathygadus antrodes is separated from the other Japanese species, *B. nipponicus* by its broader head, smaller eye and wider midline separation of the premaxillary tooth bands (Table 6). There is also a lower number of pectoral fin rays, 14–16 *cf.* 16–19, and pyloric caeca, 10–18, *cf.* 30 to >50. The teeth, although small, are prominent, particularly in small specimens, and have a strong inner curvature. The interoperculum is shallow with an expanded posterior tip (Fig. 17, 11).

According to Okamura (1970a:33) *B. antrodes* appears to be closely related to *B. cottoides*. Certainly both share a low number of pectoral fin rays (14–16 and 12–14 respectively) and both have a wide interorbital (32.2–37.1% of head length, *cf.* 26.8–33.8%), but these are also features shared with *B. spongiceps* (see Tables 2 & 3).

DISTRIBUTION. Southern Japan.

DEPTH RANGE. 792–1200m.

MATERIAL EXAMINED. USNM 50932 (Holotype), 95mm s-a, Sagami Bay; USNM 51442 (Paratype), 134mm s-a and one juvenile, *ca* 140mm TL, Sagami Bay, 99246, 83mm s-a, off Shio Misaki; 77242 & 77245, 113, 126mm s-a, off Omi Saki; 77243, 129mm s-a, 77244, 80, 65mm s-a.

Bathygadus nipponicus (Jordan & Gilbert, 1904)

Regania nipponica Jordan & Gilbert, (1902) 1904:605 (descr.).
Bathygadus garretti Gilbert & Hubbs, 1916:151 (descr.).

Gilbert & Hubbs (1916:151) separated *B. garretti* from *B. nipponicus* on the presence in the former species of a small barbel, greater number of gill-rakers, fewer dorsal fin rays, greater number of pelvic rays, narrower interorbital and small orbit.

Table 7 Counts and proportional measurements for *Bathygadus nipponicus*.

	Holotype of *nipponicus*	Types of *B. garretti* holotype	paratype
D	II10	II9	II9
Pe	17	16	19
Pl	10	10	11
GR	5+16	5+18	5+18
PC	?	?	54
s-a	217mm	180mm	156.5mm
bd	32.7	38.3	42.8
pl	28.5	broken	broken
hl	48.8	52.7	63.8
od	26.4	24.2	30.1
IO	30.6	29.4	33.3
pml	54.2	72.4	66.6
pma	26.0	26.0	23.8
pms	6.4	5.0	8.3
bl	absent	1.0	1.5

Although a barbel is present in *B. garretti* it is often hidden below the skin (see Okamura, 1984) and the development of a barbel in *Bathygadus* appears to be a primitive feature of little significance in discriminating between species. Gill-rakers on the lower arch differ by two (18 in *B. garretti*, *cf.* 16 in *B. nipponicus*), within the range of variation of other species. Again, the dorsal fin ray count differs by only one. Jordan & Gilbert (1904) miscounted the pelvic rays in *B. nipponicus* (see also Okamura, 1984:357) and both species have 10 (sometimes 11 in *garretti*). Both the orbital diameter and interorbital width of *B. nipponicus* are encompassed by the ranges of those parameters in *garretti* (see Table 7).

Okamura (1984:357) notes that *B. garretti* is separable from *B. nipponicus* in a single character, namely the presence of a mandibular barbel. Since, as detailed above, this feature does not reliably indicate specific identity, *B. garretti* is treated as a synonym of *B. nipponicus*.

DISTRIBUTION. Suruga Bay; Okinawa Trough.

DEPTH RANGE. 840–1348m.

MATERIAL EXAMINED. USNM 50931 (Holotype) 217mm s-a, Suruga Bay; 76863 & 135351 (Holotype and paratype of *B. garretti*) 180, 156.5mm s-a, Suruga Bay (35° 05′ 30″N, 138° 39′ 50″E).

Bathygadus bowersi (Gilbert, 1905)

Gadomus bowersi Gilbert (1903) 1905:659 (descr.).
Bathygadus bowersi; Gilbert & Hubbs, 1916:142 (listed).
Bathygadus bowersi; Gilbert & Hubbs, 1920:379 (in key).

The features given by Gilbert (1905) to distinguish *B. bowersi* from *B. antrodes* are lightness of colour, firmer consistency of cranial bones, differing proportions of the operculum and preoperculum, greater development of the opercular ridge and somewhat smaller scales.

Table 8 Counts and measurements for the types of *Bathygadus bowersi*.

	Holotype	Paratypes		
D	II8	II8	II8	II8
Pe	17	17	17	17
Pl	9	9	9	9
GR	8+24*	8+21	8+21	8+21
PC	?	?	?	?
s-a	139.5mm	130mm	65mm	55mm
bd	53.0	53.0	46.1	49.6
pl	30.1	broken	16.9	18.1
hl	57.3	58.4	58.4	61.8
od	33.0	21.7	23.6	23.5
io	37.5	36.0	36.8	33.6
pml	56.2	48.6	57.8	54.0
pma	24.4	25.6	29.0	27.0
pms	17.7	12.1	11.0	10.0

* given by Gilbert (1903) as 6+22 in the holotype and 6–7+22–24 in the paratypes

In their key, Gilbert & Hubbs (1920) distinguished *B. bowersi* from other species by its lack of filamentous extensions of the outer pectoral and pelvic fin rays, its wide interorbital space and dark colouration. Most of these characters are subjective and not easily quantifiable. Severe damage to the pectoral and pelvic fins of the types has made it impossible to determine whether they were filamentous. the interorbital width of *B. bowersi* has an almost co-incident ratio with that of *B. antrodes*, *viz*. 33.6–37.5% *cf*. 32.2–37.1% of the head length. Also, like *B. antrodes*, *B. bowersi* has a broad midline separation of the premaxillary dentigerous surfaces, 10.0–17.7% *cf*. 10.0–14.6% of the premaxillary length, a feature in which these species also resemble *B. cottoides* (14.2–20.0%). At its maximum, the orbital diameter (as a percentage of the head length) of *B. bowersi* exceeds that of any Indo-Pacific species, being 21.7–33.0%, *cf*. 16.7–30.1%. *Bathygadus bowersi* also has a relatively high number of gill-rakers on the first ceratobranchial (21–24), matched only by *B. antrodes* (20–24) and *B. melanobranchus* of the Atlantic (21–24). Counts and measurements for four of the types are given in Table 8.

On the basis of the six specimens which represent this species it is impossible to comment further on the variability of morphometric characters and, in view of its 'isolated' geographical position *B. bowersi* is here recognised as a distinct species.

DISTRIBUTION. Hawaiian Islands, near Bird Island and Kaui;

DEPTH RANGE. 550–1460mm.

MATERIAL EXAMINED. USNM 51658 (Holotype), 139.5mm s-a, near Bird Island, Hawaii; 51695 (paratype), 130mm s-a, 65, 55mm s-a, near Bird Island.

Key to the Atlantic species of *Bathygadus*

1 Pelvic rays 9, rarely 10 .... ***B.favosus***
Pelvic rays 7, rarely 8 2

2 Gill-rakers 5–6/19–21; interorbital width 19.7–25.0% of head length .... ***B. macrops***
Gill-rakers 5–7/21–24; interorbital width 24.5–33.9% of head length .... ***B. melanobranchus***

Key to the Indo-Pacific species of *Bathygadus*

1 Gill-rakers 5–6+16–18* 2
Gill-rakers 5–6+19–24 3

2 Interorbital width 23.5–24.4% of head length .... ***B. sulcatus* (Philippines)**
Interorbital width 29.4–32.3% of head length .... ***B. nipponicus* (Japan)**

3 Gill-rakers 5–6+19–21 4
Gill-rakers 5–8+21–24 6

4 Orbital diameter 16.0–24.5% of head length 5
Orbital diameter 30% or more of head length .... ***B. entomelas*** (Philippines)

5 Premaxillary length 56.4–61.6% of head length .... ***B. cottoides*** (Kermadec area, Indonesia, ?Indian Ocean)
Premaxillary length 52.3–55.0% of head length .... ***B. spongiceps*** (Indonesia)

6 Pectoral rays, 17 .... ***B. bowersi*** (Hawaiian-Islands)
Pectoral rays 12–15 .... ***B. antrodes*** (Japan)

* 18 occurs rarely also in *B. cottoides*.

Gadomus Regan, 1903

Gadomus Regan, 1903:459 (orthotype, *Bathygadus longifilis* Goode & Bean, 1885).

DIAGNOSIS. (Features distinguishing *Gadomus* from *Bathygadus* italicised). Head and body compressed, tail slender, without caudal fin; two dorsal fins, the first with two spiny rays, first ray reduced. *Anterior dorsal and outer pectoral and pelvic fin rays attenuated; pectoral fin with exposed nerve tract* bordering second ray. Rays of second dorsal fin longer than those of anal fin. Snout blunt; mouth large and terminal; *teeth minute*, villiform, sometimes arranged in bands on both premaxilla and dentary; *dentigerous area of premaxillae usually narrowly separated across midline. Palatine contacts only the lateral ethmoid.* Barbel present. *Interoperculum deep, trapezoidal or triangular, usually with convex posterior border.* Gill opening wide, gill-rakers on first arch slender and denticulate; gill-filaments reduced, at most half the length of the rakers (except one species); pseudobranchiae present. *Nasal bones slender and widely separated at midline.* Skull with generally *narrow interorbital width, always <25% of head length; orbit always <30% of head length. Vertebral count greater than 100.* Scales small, bearing fine reticulate pattern. *Olfactory bulbs close to olfactory lobes of brain. Four retia in swimbladder.*

Atlantic species

Iwamoto (1970) and Marshall (1973*a*) provided keys with descriptions, distributional ranges, synonymies and complete references. The following are additional data and comments.

Gadomus arcuatus (Goode & Bean), 1886

Bathygadus arcuatus Goode & Bean, 1886:158 (descr.).
Gadomus arcuatus; Gilbert & Hubbs, 1916:142 (listed).

The most obvious feature distinguishing this from other Atlantic, and indeed all other *Gadomus* species are the prolongation of the *two* outer pelvic rays rather than only the outer (second) ray, and the higher number of pectoral rays (20–25, *cf.* 13–20). In our sample, there is a higher number of gill-rakers on the first ceratobranchial than that recorded by Marshall (1973*a*), *viz.* 4–5+19–33, *cf.* 4–6+18–21. In other proportional measurements, ours correspond with the ranges given by Iwamoto (1970) and Marshall (1973*a*).

Another feature distinguishing *G. arcuatus* from the other Atlantic species is the length of the premaxillary ascending process, which is 24.3–28.0% of the premaxillary length. This contrasts with the shorter processes in *G. dispar* (19.6–24.1) and *G. longifilis* (21.0–23.6).

The gill-filaments are exceedingly short, being only 25% of the gill-raker length.

Marshall (1973*a*) drew attention to the similarity in dentition between *G. arcuatus* and *G. denticulatus* (Indonesia). This similarity lies in an upward expansion of the premaxillary dentigerous area onto the medial ascending process. However, this is not uncommon in *Gadomus* species, particularly in large individuals. The rows of premaxillary teeth in *G. arcuatus* appear to be more regularly arranged than in other species.

We have found no specimens from localities that alter the distribution given by Marshall (1973*a*) namely between the Equator and 30°N.

Depth range. 610–137m (Marshall, 1973*a*).

Material examined. BMNH 1969.6.26:3264, 160mm s-a (*ca* 347mm TL), off Honduras; 1963.2.25:2–3, 57.5 & 68mm s-a, Caribbean; USNM 212158, 83mm s-a, off Nicaragua; 212160, 99mm s-a, Gulf of Mexico; 3658, 175mm s-a (*ca* 485mm TL), 126mm s-a, 179mm s-a; Uncat. 133mm s-a, off Mississippi delta.

Counts and measurements for a sample of ten specimens are given in Table 9.

Table 9 Counts and proportional measurements for ten specimens of *Gadomus arcuatus*. Ranges in square brackets are those given by Marshall (1973a).

	Range	Mean	
D	II10–11		
Pe	20–22		
Pl	8		
GR	4–5+19–23		
Pc	25–30		
s-a	83–179mm		
bd	40.9–51.1	46.5	
pl	32.4–53.0	43.4	
hl	50.0–55.5	52.1	
od	20.6–27.0	23.4	[17.8–26.7]
io	17.0–21.8	17.1	[16.7–20.0]
pml	58.0–51.6	55.7	[52.0–57.3]
pma	24.3–28.0	24.2	
pms	4.6–7.8	4.9	
bl	67.1–94.8	80.1	[65.6–87.3]

Gadomus dispar (Vaillant, 1888)

Hymenocephalus dispar Vaillant, 1888:221 (descr.).
Gadomus dispar; Gilbert & Hubbs, 1916:142 (listed).

In Marshall's (1973*a*) key, *G. dispar* is separated from *G. longifilis* by its fewer gill-rakers (20–21, *cf.* 27–31) and higher number of pectoral rays (18–20, *cf.* 14–16). The other feature given by Marshall to separate the two species is the interorbital width, given as 15–17% of the head length in *G. dispar* and 21–25% in *longifilis*. In our sample of *dispar*, the proportion is 18.6–19.1% and in *longifilis* 19.7–24.8%. Thus there is very nearly a continuum rather than a wide gap in this parameter. Nevertheless, it is sufficiently distinct to separate the two species.

Two other parameters that separate *dispar* from the other Atlantic species are length of the head and diameter of the orbit. The head length of *dispar* is the shortest of the three species, being 47.0–49.5% of the snout to anal fin distance, *cf.* 50–55.5% in *arcuatus*, and 52.5–55.6% in *longifilis*. The horizontal diameter of the orbit is the longest of the three species, *viz.* 27.6–29.5% of the head length (given by Marshall as 26.8–31.6%), *cf.* 20.6–27.0% in *arcuatus* and 23.5–27.7% in *longifilis*.

In only one specimen examined is the pectoral fin complete, measuring 91.0% of the snout-anal fin distance. It is thus longer than the pectoral fin of the other two species, *viz.* 32.4–53.0% in *arcuatus* and 57.8–63.2% in *longifilis*.

We are unable to corroborate Marshall's 1973*a*) opinion that *G. dispar* is closely related to *G. denticulatus* of the Philippines.

Comparisons between *G. dispar* and *G. longifilis* are given in Table 10.

Material examined. USNM 216159, two specimens 100 & 108mm s-a, off Honduras, 14° 10′N, 81° 50′W; USNM Uncat., 112mm s-a, off Nicaragua, 12° 25′N, 82° 15′W.

Distribution. Western and eastern Atlantic, Caribbean Sea, and off Morocco.

Depth range. 548–1105mm (see Marshall, 1973*a*).

Gadomus longifilis (Goode & Bean, 1885)

Bathygadus longifilis Goode & Bean, 1885:599 (descr.).
Hymenocephalus longifilis; Vaillant, 1888:218 (descr.).
Gadomus longifilis; Regan, 1903:459 (type species designation).

Apart from the higher number of gill-rakers on the first ceratobranchial (27–31, *cf.* 20–21 in *dispar* and 18–23 in *arcuatus*), the lower number of pectoral fin rays (13–16, *cf.* 17–22 in the other two species), and the modally wider interorbital (22.7% of head length, *cf.* 17.1% in *arcuatus* and 18.8% in *dispar*), *G. longifilis* can also be distinguished from the other Atlantic species by the shorter barbel, which is only 40.0–50.0% of the head length, *cf.* 67.1–94.8% in *G. arcuatus* and 75.4–90.0% in *dispar*. The gill-filaments are, at the centre of the ceratobranchial, only 20% of the length of the gill-rakers; the shortest of any *Gadomus* species.

Pyloric caeca are few, varying from 5 in a specimen of 37.3mm s-a, and 9 in one of 49.0mm, to 12 in larger specimens. This is the lowest number of caeca possessed by any of the Atlantic species.

The premaxillary teeth are relatively well-developed, in common with the other Atlantic species, and arranged in a narrow band; teeth on the dentary are reduced to a single row posteriorly.

Table 10 Counts and proportional measurements for three specimens of *Gadomus dispar* and fifteen specimens of *G.longifilis*. Ranges in square brackets are those given by Marshall (1973a).

G. dispar	Range	Mean	
D	II9–11		
Pe	17–18		
Pl	8		
GR	4+20–21		
Pc	35+		
s-a	100–112mm		
bd	40.1–41.6	40.3	
pl	91.0 (others broken)		
od	27.6–29.5	28.3	[26.8–31.0]
io	18.6–19.1	18.8	[15.2–17.1]
pml	52.2–54.7	53.7	[51.6–56.3]
pma	19.6–24.1	22.0	
pms	5.0–5.8	(two only measured)	
bl	75.4–90.0	84.2	
G. longifilis			
D	II9–10		
Pe	17–18		
Pl	8		
GR	6–8+27–29		
PC	12–15		
s-a	37.3–75.5mm		
bd	35.3–45.2	39.7	
pl	57.8–63.2	60.5	
hl	52.5–55.6	53.6	
od	23.5–27.7	26.2	[23.1–28.0]
io	19.7 24.8	22.7	[21.1–25.0]
pml	52.7 56.8	55.1	
pma	21.0–23.6	22.0	
pms	4.7–5.2	4.9	
bl	40.0–50.0	43.8	[31.6–40.0]

According to Marshall (1973*a*), *G. longifilis* is most closely related to the Indo-Pacific *G. multifilis*, although we have found no evidence to support this assumption.

Gilbert & Hubbs (1920:406) note that records of *G. longifilis* from the Indian Ocean are probably misidentifications. Marshall (1973*a*) supported this view by citing a specimen of Alcock, from off the Maldives, which Marshall identified as *G. multifilis*. Regardless of the correct identity of the Indian Ocean species (p. 196) our findings support those of previous authors in failing to locate any specimen of *longifilis* from an Indo-Pacific locality.

DISTRIBUTION. Gulf of Mexico, Caribbean, Straits of Florida, Azores, Canary Islands and off Mauritania, west coast of Africa.

DEPTH RANGE. 630–2165m (see Marshall, 1973*a*).

MATERIAL EXAMINED. BMNH 1963.2.25:7–17, ten specimens, 37.3–75.5mm s-a (largest specimen *ca* 230mm TL) 'Oregon' Stn 3562; 1963.2.25:18–19, 61.0, 62.5mm s-a, 'Oregon' Stn 3586; USNM 37338 (syntypes), 67.4 & 68.0mm s-a, 28°N 87°W; USNM Uncat. 65.5mm s-a, 'Oregon' Stn 4040.

Gadomus capensis (Gilchrist & von Bonde) 1924

Bathygadus capensis Gilchrist & von Bonde, 1924:13 (descr.).
Bathygadus fumosus Barnard, 1925*a*:500 (published April); 1925*b*:333 (published June) (descriptions).
Gadomus capensis; Marshall, 1973*a*:519 (in key).
Gadomus fumosus; Marshall, 1973*a*:519 (in key).
Gadomus capensis; Iwamoto, 1986:335 (synonymisation).

Iwamoto (1986) states that Heemstra's examination (reported *in litt.*) of the types of *B. capensis* and *B. fumosus* reveal no differences other than the rudimentary barbel of the former (said by Gilchrist & von Bonde to have been absent). Further examination of types of both specimens supports Heemstra's findings and Iwamoto's synonymy (Table 11).

Gadomus capensis is undoubtedly closely related to the species recognised here as *G. 'multifilis'* from the east African coastal waters and other Indian Ocean localities. It differs, however, in a greater body depth (46.4–48.2%, *cf.* 33.8–43.6% of s-a length), longer premaxilla (57.1–60.4%, *cf.* 55.2–58.4% head length), narrower midline separation of the premaxillary dentigerous surfaces (3.5–6.8%, *cf.* 8.2–13.1% premaxillary length) and shorter barbel. The length of the pectoral fin is virtually the same, which distinguishes *capensis* and '*multifilis*' from other Atlantic species. With *G. longifilis* and *G. multifilis*, *G. capensis* shares a high number of gill-rakers (6–7+25–7), a feature which also sets it apart from *G. furvescens* which has 6–7+20–22 rakers. There is no trace of any dark pigmentation on the dorsal and pectoral fins which appears to be a characteristic of the Indian Ocean *G. multifilis* (see p. 196).

Also identified aş *G. capensis* is a specimen from off Cape Point, previously determined by Gilchrist as *Bathygadus (Gadomus) furvescens*. This misidentification draws attention to the possibility that those specimens listed by Gilchrist & von Bonde (1924) under *Bathygadus melanobranchus* (*B. furvescens* was treated by those authors as a synonym of that species) may well include *Gadomus capensis*. Pakhurov (1980) records *G. capensis* (cited as *G. fumosus*) from the mid-Atlantic ridge. If these specimens have been correctly identified then the species' distribution encompasses both Atlantic and Indian Oceans.

DISTRIBUTION. Table Bay to Mozambique (Iwamoto, 1986); Atlantic (Pakhurov, 1980).

DEPTH RANGE. 750–1450m.

MATERIAL EXAMINED. RUSI 36 (Holotype), 94mm s-a, off Cape, Stn 450; BMNH 1927.12.6:14 (syntype of *G. fumosus*), 84mm s-a, off Cape Point; 1904.5.28:11, 74.2mm s-a, 34 miles north-east of Cape Point.

Table 11 Counts and proportional measurements for the types of *Gadomus capensis* and *G. fumosus*.

	capensis	*fumosus*
D	II9	II8
Pe	17	18
Pl	8	8
GR	7+25	6+25
PC	?	19
s-a	94mm	84mm
bd	48.2	46.4
pl	123.9	84.5 (broken)
hl	52.1	51.1
od	25.5	23.2
io	23.4	23.2
pml	57.5	60.4
pma	21.4	21.1
pms	3.5	5.7
bl	1.8	6.9

Indo-Pacific species

Gadomus furvescens (*Alcock, 1894*)

Bathygadus furvescens Alcock, 1894:128 (descr.); 1895:pl.16, fig.1.
Bathygadus furvescens; Norman, 1939:47 (synonymy; comments).
?*Bathygadus melanobranchus*; Brauer, 1906 (*non*-Vaillant): 272 (descr.); Barnard, 1925*b*:334 (descr.).

This species is here referred to the genus *Gadomus* on the basis of its long filamentous dorsal, pectoral and pelvic fin rays; a barbel (albeit reduced); a well-developed branch of the RLA-P nerve passing along the second pectoral fin ray; narrow midline separation of the premaxillary dentigerous surfaces and deep, nearly square interoperculum.

Alcock (1894:199) was incorrect in stating that a barbel was lacking in *G. furvescens*; a small barbel is present in the syntype we have examined. Of the other twelve specimens examined, eight have small or minute barbels, but in the other four, a barbel is totally lacking. There is apparently no correlation between barbel length and head length, nor between interorbital width and head length, or orbital diameter and head length.

The teeth of *G. furvescens* are coarse and rather large and are not arranged in regular rows on the premaxilla. The separation between the dentigerous tips of the premaxillae is variable (3.7–6.5% of premaxillary length) but is one of the narrowest (3.7%) of all *Gadomus* species. The length of the premaxilla is also variable (46.2–60.0% of head length) and the higher figure is the maximum premaxillary-head length ratio recorded in *Gadomus*.

The gill-filaments are long, compared with those of other species, being 50–93% of the length of the gill-raker. In this feature, *G. furvescens* differs from other *Gadomus* species.

The membranes of the dorsal fins are noticeably black and in this respect resemble those of the Indian Ocean *G. multifilis*. *Gadomus furvescens* differs from *G. multifilis* and *G. capensis*, however, in having fewer gill-rakers on the ceratobranchial (20–22, *cf.* 25–27), shallower body depth and shorter pectoral fin (see Table 12 for proportional measurements).

It seems likely that most of the references to Indian Ocean *Bathygadus melanobranchus* refer to *G. furvescens* (but see also p. 194 under *Gadomus capensis*). Specimens identified as *Bathygadus furvescens* by Gilbert & Hubbs (1920:338) from the Philippines do not belong to this species and should be referred to *Bathygadus cottoides* along with the *B. melanobranchus* of Weber, 1913.

DISTRIBUTION. Gulf of Aden, Maldives, Andaman Sea, Bay of Bengal.

DEPTH RANGE. 790–1295m.

MATERIAL EXAMINED. BMNH 1896.9.11:2 (Syntype), 150.0mm s-a, Arabian Sea, 9° 34′N, 73° 36′E; 1939.5.24:675-6, 35.5 & 122.5mm s-a, plus one specimen of 64mm TL, 13mm hl, (tail broken), too damaged to measure, Gulf of Aden; 1939.5.24: 673–74, 84.5 & 53mm s-a, Maldive area; 1939. 5.24:669, *ca* 275mm TL (not measured), Gulf of Aden; 1939.5.24:670–72, 88mm s-a and three other specimens not measured but used in counts, one badly disintegrated, one *ca* 140mm TL, 35.5mm hl, one *ca* 255mm TL, *ca* 63mm hl, Gulf of Aden.

Table 12 Counts and proportional measurements for a syntype of and five other specimens of *Gadomus furvescens*.

	Syntype	5 specimens, BMNH 1939,5,24:699; ex:670–76	Mean
D	II10	II9–10	
Pe	15	14–15	
Pl	8	8	
GR	6+22	6–7+20–21	
PC	*	20–28(n3)	
s-a	150mm	35.5–122.5mm	
bd	38.5	29.6–40.8	31.6
Pl	32.0	49.7–53.2(n3)	45.0
hl	50.5	53.8–61.9	55.6
od	23.2	21.6–27.3	24.4
io	20.9	19.6–27.3	22.5
pml	55.4	46.2–60.0	57.4
pma	22.6	20.5–26.8	22.6
pms	6.5	3.7–9.3	6.2
bl	5.4	0.7–3.0(n3)	2.7

* Gut removed, but given as 20 by Alcock (1894).

Gadomus multifilis (Günther, 1887)

Bathygadus multifilis Günther, 1887:155 (descr.).
Bathygadus longifilis; Alcock, 1890 (*non* Goode & Bean):302; 1891:123 (descr.); Chun, 1900:504 (descr.); Brauer, 1906: 270 (descr.).
?*Gadomus* sp. Gilbert & Hubbs 1916:153 (descr. Japan).
Gadomus multifilis; Gilbert & Hubbs, 1920:406 (descr.).
Bathygadus (Gadomus) multifilis; Weber & de Beaufort, 1929:23 (descr.).
Gadomus multifilis; Norman, 1939:48 (partial descr.).
Gadomus multifilis; Okamura, 1970*a*:27 (descr. of Philippine specimen).

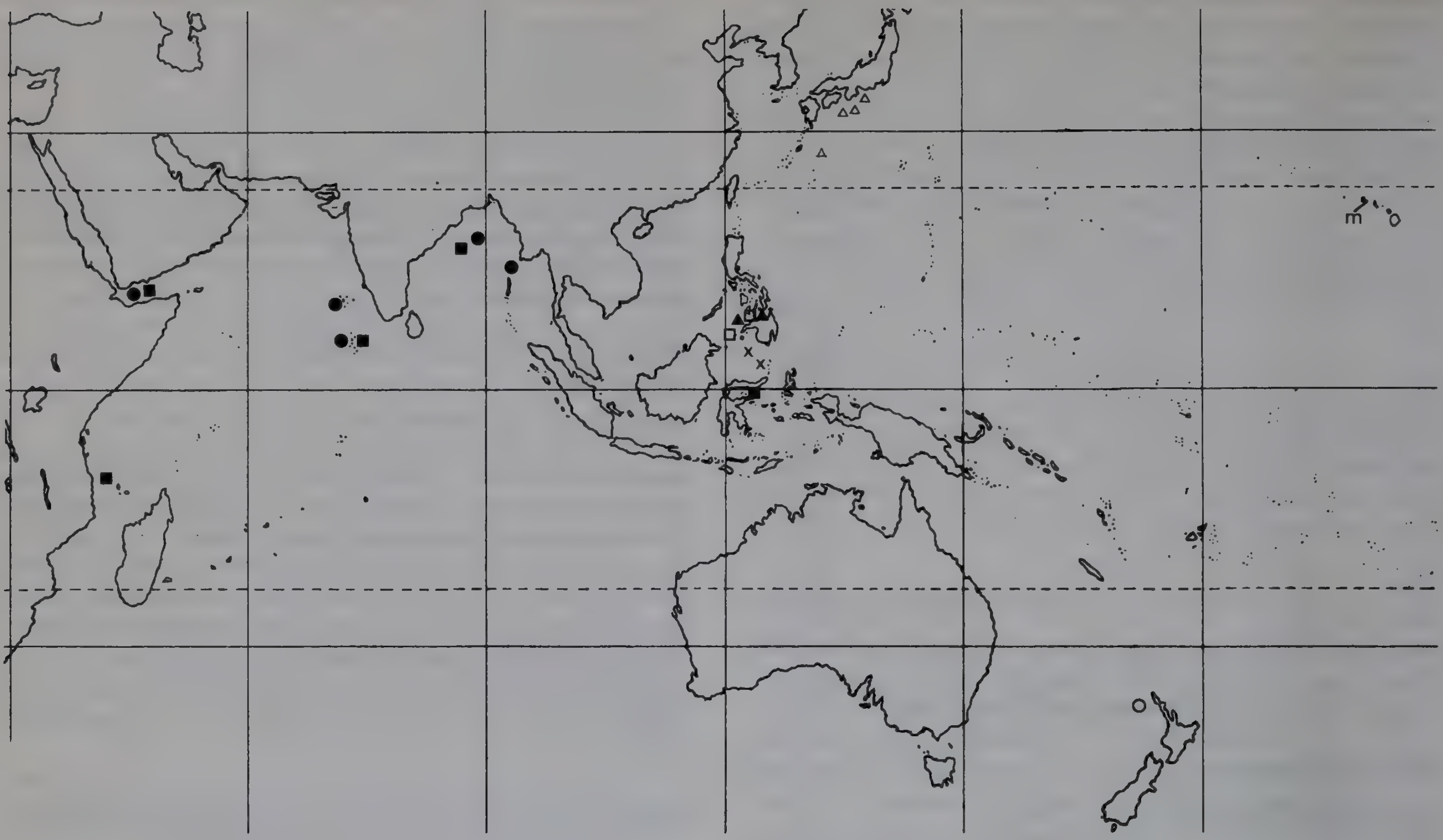

Fig. 32 Indo-Pacific distribution of *Gadomus* species. □=*G. denticulatus*, O=*G. aoteanus*, △=*G. colletti* (Japan), ●=*G. furvescens*. ■=*G. multifilis*, ▲=*G. magnifilis*, X=*G. introniger*, m=*G. melanopterus* (Hawaii).

The type specimen is recorded from south of the Philippines; it is a juvenile of 123.5mm TL (tail missing). According to Gilbert & Hubbs (1920:406) the species identified as *G. longifilis* by Alcock, Brauer and Chun from the Indian Ocean is probably *G. multifilis*. Marshall (1973*a*) agreed with this view, in identifying one of Alcock's specimens from the Maldive area as *multifilis*.

The present study confirms that the Indian Ocean species differs from *G. longifilis* and on the basis of corresponding meristic and morphometric features it would appear to be *multifilis*. However, the type and other *multifilis* specimens examined, have, compared with all other species, a longer head (53.2–60.4% s-a, *cf.* 46.6–55.6% in others); the width separating the dentigerous areas of the premaxillae is also greater (8.2–13.1% *cf.* 3.9–6.0% in others). In this latter feature *G. multifilis* approaches the condition observed in *Bathygadus*. Counts and measurements are given in Table 13.

The Indian Ocean specimens assigned to *G. multifilis* have a very dark anterior area on the dorsal fin membrane and black pelvic rays. The branchiostegal membrane is also black with a white proximal region. Such a pigmentation pattern is lacking in the type specimen, although this may simply be due to its long period of preservation. The specimen recorded from Japan by Gilbert & Hubbs (1916) as *Gadomus* sp. and later (1920) referred by them to *multifilis* cannot now be traced, although their (1920) specimen reported from the Philippines certainly belongs to that species and it is upon this that Okamura (1970*a*:26–29) based his description. Okamura noted (presumably referring to Gilbert & Hubbs, 1916), that only one specimen is known from Japanese waters. It is doubtful, however, that it represented *multifilis* since according to Gilbert & Hubbs it had a higher number of gill-rakers and a narrower interorbital width. The record of *G. multifilis* from the Emperor sea mount chain (Novikov *et al.*, 1980) is also doubtful; this (these) specimens probably represent the northward extension of the Hawaiian species, *G. melanopterus*.

Gilbert & Hubbs (1920:406) thought that *G. melanopterus* might be synonymous with *G. multifilis*. However, *melanopterus* differs in its higher number of pelvic rays (9,*cf.* 8), a narrower midline separation of the dentigerous areas of the premaxillae, shorter head and greater number of gill-rakers (7+27, *cf.* 6+25).

Table 13 Counts and proportional measurements of the holotype of *Gadomus multifilis* and eight other specimens.

	holotype (Philippines)	7 specimens from Indian Ocean localities	1 specimen from Molucca Sea (USNM 99447)
D	II8	II8	II9
Pe	15	16	16
Pl	8	8	8
GR	6+25	6+25 6+25	6+25
PC	?	25 (1 spec.)	15
s-a	42mm	43–71.5mm	63mm
bd	36.9	33.8–43.6	43.6
pl	broken	109.6–123.0	broken
hl	57.1	53.2–60.4	60.3
od	25.0	25.8–27.3	24.2
io	20.8	19.0–25.0	22.3
pml	52.0	57.1–58.4	55.2
pma	21.6	20.6–22.1	19.0
pms	10.4	8.2–13.1	14.2
bl	47.9	63.0–68.8	63.0

DISTRIBUTION. Indian Ocean, Philippines.

DEPTH RANGE. 760–1170m.

MATERIAL EXAMINED. BMNH 1887.12.7:146 (Holotype), 42mm s-a, south of Philippines; 1939.5.24:682, 43mm s-a, Zanzibar area; 681, 74mm s-a, Maldive area; 683, 24mm s-a, Gulf of Aden; 1898.7.13:16, 71.5mm s-a, Maldives; USNM 99447, 63mm s-a, 0° 04′S, 121° 36′E, East Philippines; BMNH 1939.5.24:678–80, 62, 66, 71mm s-a, Maldive area.

Gadomus aoteanus McCann & McKnight 1980

Gadomus aoteanus McCann & McKnight, 1980:21 (descr.).
Bathygadus longifilis; McCann, 1972 (*non* Goode & Bean, 1886):620

Described from three specimens, the meristics and morphometrics of two of which were published in the description. These measurements have here been converted to proportional values (Table 14).

According to McCann & McKnight, *G. aoteanus* is related to the Philippine species *G. introniger* from which it supposedly differs in having a longer head and upper jaw, fewer pectoral fin rays and one more pelvic ray. In fact only one specimen of *G. aoteanus* has a head length greater than *G. introniger* and the upper jaw (taken as premaxillary length) is *shorter* than that of *introniger* (51.8–50.8%, *cf.* 52.3–56.1% of head length). *Gadomus aoteanus* differs from all the Philippine species in having a shorter upper jaw, a broader interorbital (width recorded from only one specimen by McCann & McKnight; *viz.* 25.0% of head length *cf.* 15.5–11.5% in Philippine species and 23.1% in the Hawaiian species, *G. melanopterus*) and in having a higher number of gill-rakers (7+25 *cf.* 4–6+20–23). As in *G. melanopterus*, *G. aoteanus* has 9 pelvic fin rays. It differs from other Indo–Pacific *Gadomus* in having a relatively short barbel (16.6–18.6% of head length, *cf.* 22.1–83.3%).

At present, this species is recorded only from the southern Norfolk Ridge off the North Island of New Zealand at a depth range of 970–1232m.

No material was available for this study.

Table 14 Counts and proportional measurements for *Gadomus aoteanus* compiled from data given by McCann & McKnight (1980)

D III0; Pe 14–15; Pl 9; GR 7+25; PC 14–100+

s-a	102mm	106mm
bd	42.1	47.1
pl	107.8	132.0
hl	52.9	55.6
od	22.2	22.7
io	25.0	?
pml	51.8	50.8
bl	16.6	18.6

Gadomus magnifilis Gilbert & Hubbs, 1920

Gadomus magnifilis Gilbert & Hubbs, 1920:398 (descr.).

Known only from the holotype and two paratypes taken off northern Mindanao.

Gilbert & Hubbs (1920) considered this species to be most closely related to *G. denticulatus* from which, according to those authors, it is distinguished by 'marked differences'. There is, however, an overlap in all our measurements and counts between the two species (with the exception of the head length). In *G. magnifilis*, the head is 51.7–55.2% of the snout-anal fin distance, in contrast to a range for *G. denticulatus* of 46.6–48.9% and *G. introniger* of 48.0–53.2%. *Gadomus magnifilis* resembles *G. introniger* in the broad midline separation of the dentigerous surfaces of the premaxillae (5.0% of premaxillary length, *cf.* 6.0%). The most striking distinguishing feature of *G. magnifilis* is the length of its second pectoral fin ray, which is 141–142.8% of the snout-anal fin distance compared with a maximal measurement of 126.0% in *G. denticulatus*.

Both *G. magnifilis* and *G. denticulatus* possess similar dentition. The teeth are minute, giving an almost smooth appearance to the premaxillary and dentary dentigerous surfaces and both share the same degree of expansion of the premaxillary dentigerous surface near to the symphysis. Both species also possess a short, deep interoperculum with a shallowly concave posterior border (Fig.17g,j).

With the collection of more material it may become apparent that *G. magnifilis* and *G. denticulatus* are conspecific. However, on the basis of the differences given above *magnifilis* is here recognised as a distinct species.

DISTRIBUTION. Off Mindanao, Philippines.

DEPTH RANGE. 914–1260m.

MATERIAL EXAMINED. USNM 78208 (Holotype), 112mm s-a, off northern Mindanao, Philippines; 221089 (paratype), 75.5mm s-a southern Leyte Island; 078234, Sulu Sea (too damaged to record measurements). Meristic and morphometric data are given in Table 15.

Table 15 Counts and proportional measurements of the holotype (USNM 78208) and paratype (USNM 221089) of *Gadomus magnifilis*.

	Holotype	Paratype
D	II10	II9
Pe	17	17
Pl	8	8
GR	5+22	6+21
PC	?	22
s-a	112mm	75.5
bd	42.8	45.0
pl	142.8	141.0
hl	51.7	51.6
od	19.8	25.6
io	17.2	17.9
pml	57.7	56.4
pma	22.5	22.7
pms	5.9	5.0
bl	60.3	79.4

Gadomus denticulatus Gilbert & Hubbs, 1920

Gadomus denticulatus Gilbert & Hubbs, 1920:393 (descr.).
Bathygadus (Gadomus) denticulatus; Weber & de Beaufort, 1929:21 (descr. after Gilbert & Hubbs).
?*Bathygadus longifilis*; Weber, 1913:173 (descr.).

Known from the holotype and ten paratypes from the Philippines and off Borneo.

Gilbert & Hubbs (1920:392–3) distinguish *denticulatus* from *G. colletti* on the basis of differences in the posterior expansion of the premaxillary tooth bands. 'Expanded posteriorly' is here understood to mean where the dentigerous surface expands somewhat dorsad onto the postmaxillary process of the premaxilla. This is not, however, a valid diagnostic feature, since it appears to be phenotypically variable. The anterior region of the dentigerous surfaces of both the premaxilla and dentary are broadly expanded in *G. denticulatus* whereas in other species they remain constantly narrow or are only slightly broadened.

The number of pyloric caeca is also given by Gilbert & Hubbs (1920) as a distinguishing feature of *denticulatus* and *colletti*. For the former species they give 61–75 and for the latter, 95. However, the number of caeca in *denticulatus* appears to be more variable, ranging from 30 to over 70.

In most morphometric parameters, *denticulatus* shows overlap with other species; the exceptions being the head length and interorbital width. The head is 46.6–48.9% of the snout and anal fin distance, *cf.* 48.0–55.2% in other Philippine species, (but 47.9–49.1% in *G. colletti*; see Table 16). The interorbital width is narrow, being 15.5–17.1% of the head length, *cf.* 17.2–22.5% in Philippine species and 17.7–19.1% in *G. colletti*.

As noted under *G. magnifilis*, the interopercular morphology of the two species is virtually identical and in this respect differs from that of *G. colletti* where the interoperculum is more extended anteriorly and rounded posteriorly (*cf.* Figs 17f,j).

Gilbert & Hubbs (1920) synonymised Weber's (1913) *G. longifilis* with *G. denticulatus*, an action followed by Weber & de Beaufort (1929). We are less certain, however, of the correct identity of Weber's material since Weber & de Beaufort (1929) give a gill-raker range of 17–26. Only in *G. melanopterus*, from Hawaii is there such a high number of rakers and certainly such a broad range has not been recorded in other *Gadomus* species.

Table 16 Counts and proportional measurements for the holotype, and nine paratypes of *Gadomus denticulatus*

	Holotype	Paratypes	Mean
D	II9	II9–11	
Pe	17	16–18	
Pl	8	8	
GR	5+17	4–5+17–20	
PC	?	30–70+	
s-a	120mm	70.5–114mm	
bd	41.6	33.9–41.4	38.4
pl	126.0	96.4–126.0	115.6
hl	46.6	46.9–48.9	47.7
od	25.0	26.3–29.1	26.8
io	15.5	16.4–17.1	16.4
pml	53.5	50.4–57.1	53.5
pma	26.6	20.0–27.7	24.7
pms	4.0	2.0–3.0	3.0
bl	69.9	70.0–83.3	77.5

DISTRIBUTION. Between the Philippine islands and the Sulu Sea.

DEPTH RANGE. 194–747m (the North Bornean depth distribution for '*longifilis*' given by Weber & de Beaufort is 475–759m).

MATERIAL EXAMINED. USNM 078207 (Holotype), 120mm s-a, off northern Mindanao; 148985 (paratypes), 70.5 & 73.5mm s-a; 148977–83 (paratypes), 72–114mm s-a, Sulu and Mindanao Seas, off North Borneo, vicinities of Bohol, Leyte, Gillololo and Makyan Islands, Luzon, Mindoro and between Cebu and Leyte.

Gadomus introniger Gilbert & Hubbs, 1920

Gadomus multifilis; Radcliffe, 1912 (*non* Günther, 1867):106 (part).
Gadomus introniger Gilbert & Hubbs, 1920:401 (descr.).
Bathygadus Gadomus) introniger; Weber & de Beaufort, 1929:21 (descr. after Gilbert & Hubbs).

Known from the holotype and twelve paratypes, the type locality Buton Strait, near Celebes (see Table 17).

According to Gilbert & Hubbs (1920) *G. introniger* differs from *G. denticulatus* and *G. colletti* in its coarser dentition. The 'coarseness' of the dentition is, if judged by the number of teeth occurring on any particular area of the premaxilla or dentary, phenotypically variable and some specimens of *introniger* have the same 'coarseness' as those of *denticulatus*. In some individuals the teeth on both the premaxilla and dentary may be longer and more pronounced along the outer margin of the bones.

In most meristics and morphometric parameters *G. introniger* overlaps with those of other Philippine species. However, in the width of the interorbital, *introniger* is distinct, (22.0–22.5% of the head length, *cf.* 15.5–21.1% in the other three Philippine species, *magnifilis, denticulatus* and *multifilis*). *Gadomus introniger* also has a wider midline separation of the premaxillary dentigerous surfaces than *G. denticulatus* and *G. colletti* (6.0–6.1% of premaxillary length, *cf. 3.1–4.4%). The interoperculum is also longer than in other species and has a rounded posteroventral margin (Fig. 17i).*

Twenty pyloric caeca were counted in one specimen.

Table 17 Counts and proportional measurements for the holotype and three paratypes of *Gadomus introniger*

	Holotype	Paratypes	Mean
D	II9	II10	
Pe	18	17	
Pl	8	8	
GR	5+22	5–6+21–23	
PC	?	20 (1 spec.)	
s-a	124mm	57–102mm	
bd	31.4	34.2–44.9	37.1
pl	100.8	108.0 (1 spec., others broken)	
hl	50.8	48.0–53.2	50.9
od	23.8	22.0–27.1	23.9
io	22.2	22.0–22.5	23.0
pml	52.3	55.1–56.1	54.6
pma	18.1	20.0–24.0	21.6
pms	6.0	not measured	
bl	15.8 (broken)	51.6–69.0	60.5

DISTRIBUTION. Philippine Sea.

DEPTH RANGE. 540–1260m.

MATERIAL EXAMINED. USNM 78209 (Holotype), 124mm s-a, Buton Strait, near Celebes; 99484 (paratype), 83.5mm s-a, Malavantuan Island; 99485 (paratype), 57mm s-a, North Island; 99486 (paratype), 102mm s-a. The other paratypes are in too poor a condition to provide accurate measurements but have been used for fin-ray and gill-raker counts. Only in specimen 99485 could pyloric caeca be counted, as it had been dissected to expose the everted stomach; in other specimens the caeca are obscured by eversion.

Gadomus colletti Jordan & Gilbert, 1904

Gadomus colletti Jordan & Gilbert, (1902) 1904:603 (descr.).
Bathygadus colletti; Weber, 1913:172 (listed).

Known from the holotype collected in Suruga Bay, Japan and from several other specimens collected subsequently from around southern Japan (see Okamura, 1970*a*; 1982; 1984). According to Gilbert & Hubbs' (1920) ke, *G. colletti* can be separated from other *Gadomus* species on the posterior expansion of the premaxillary teeth, 'colour lighter', 'head firmer' and pyloric caeca numbering 95.

The variability of the posterior width of the premaxillary dentigerous surface has been remarked above, under *G. denticulatus*. Insufficient data were available in the present study to judge 'lightness of colour' as a diagnostic feature, although from Okamura's (1984) description of fresh material, the body is purplish-pink or pinkish, being lighter on its ventral surface. The firmness of the head is too imprecise a character to be diagnostic. Okamura (1970*a*:23), in his key separating *G. colletti* from *G. multifilis*, modified this feature to that of sensory canals being less developed in *colletti* than in *multifilis*.

The number of pyloric caeca is higher than in other species; it has not been possible to confirm Gilbert & Hubbs (1920) count since the stomach of the type of *G. colletti* has been removed, as has that of the other two specimens examined.

Table 18 Counts and proportional measurements for the holotype and two other specimens of *Gadomus colletti*. Ranges in square brackets indicate those figures given by Okamura (1982; 1984) for a total of 15 specimens of 148–420mm TL.

	Holotype	USNM135352	USNM150253	
D	II10	II9	II10	
Pe	21	19	19	[18–22]
Pl	8	8	8	
GR	4+20	5+20	4+20	[3–5+20–22]
PC	*	?	?	
s-a	120mm	116.3mm	66.0mm	
bd	36.2	39.6	43.3	
pl	89.1	89.7	75.7	
hl	49.1	44.8	50.0	
od	23.7	22.4	30.3	[22.2–32.8]
io	17.7	20.1	19.6	
pml	54.4	50.0	52.1	[50.0–58.8]
pma	26.5	19.2	17.4	
pms	3.1	5.7	?	
bl	76.2	88.4	81.8	[75.0–90.6]

* given as 90 by Jordan & Gilbert (1902).

The most significant characters separating *G. colletti* from other Indo-Pacific species appear to be the higher number of pectoral fin rays, *viz*. 18–22, *cf*. 16–18; the second pectoral ray is not as attenuated as in other species (75.0–89.1%, $\bar{x}$ 85.3% of snout to anal fin distance, *cf*. 96.4–142.8% $\bar{x}$ 115.0% in other species). The length of the barbel is also longer than in other species, being 75.0–90.6% of the head length, *cf*. 16.6–83.3%. The interoperculum is deep with a broadly rounded posterior border (Fig. 17f). Counts and proportional measurements for the holotype and two other specimens are given in Table 18.

DISTRIBUTION. confined to the Pacific coast of Japan and along the Kyushu-Palau Ridge.

DEPTH RANGE. 335–1200m (Okamura, 1982; 1984).

MATERIAL EXAMINED. USNM 50930 (Holotype), 120mm s-a (*ca* 330mm TL), Suruga Bay, Japan; 135352, 116.3mm s-a (*ca* 300mm TL), Suruga Gulf; 150253, 66mm s-a (*ca* 190mm TL), Suruga Gulf.

Gadomus melanopterus Gilbert 1905

Gadomus melanopterus Gilbert, (1903) 1905:23 (descr.).
Melanobranchus micronema Gilbert, *ibid*.:661 (descr.).
Bathygadus melanopterus; Weber, 1913:172 (listed).
Gadomus melanopterus; Gilbert & Hubbs, 1916:142 (listed).

Known from two specimens from the Hawaiian Islands.

Separated by Gilbert & Hubbs (1920) from *G. multifilis* by 9, *vs* 8 pelvic fin rays, absence of pseudobranchiae, and the scapular foramen being entirely within the coracoid. The variability of the latter feature is discussed on p. 174, and, in fact, pseudobranchiae are present in the type specimen. The presence of 9 pelvic rays is, however, unusual and occurs elsewhere only in *G. aoteanus* (but see below).

We refer *Melanobranchus micronema* Gilbert to the synonymy of this species. Gilbert & Hubbs (1916) listed *micronema* as a species of *Bathygadus*, which they later included (1920) in the subgenus *Melanobranchus*, separating the species from *B. filamentosus* on the basis of its higher number of gill-rakers, presence of a barbel and longer orbit. The present investigation concludes that *micronema* belongs to *Gadomus* since it possesses a barbel (albeit reduced), has prolonged fin rays, narrow midline separation of the premaxillary dentigerous surfaces, and the interopercular shape characteristic of that taxon (Fig. 17h). It differs from *G. melanopterus* in having 8 rather than 9 pelvic rays; 6+29, *cf*. 7+27 gill-rakers on the first arch and a reduced barbel. Otherwise its proportional measurements agree with those of *melanopterus*, particularly in the equivalent sizes of the orbital diameters and interorbital widths (see Table 19).

Like *G. multifilis* and *G. aoteanus*, *G. melanopterus* has a high number of gill-rakers (6–7+27–29, *cf*. 6+25 in *multifilis* and *aoteanus* and 4–6+17–23 in other species). The jaw teeth are well-developed in comparison with the minute teeth of the Philippine species and the dentigerous area of the dentary is narrower than in those species. The interpremaxillary dentigerous space is narrow (3.0–3.5% of the premaxillary length). The interorbital width is also narrow (23.1–25.6% of head length), although not as narrow as in some individuals of *G. magnifilis* and *G. introniger* (see Tables 15 & 17). Likewise, the premaxillary ascending process is short, 17.8–19.6% of the premaxillary length, *cf*, 20.0–24.0% in other species, and is as short in only one specimen of *G. introniger* (18.1%). The length of the barbel is also shorter than that of most other Indo-Pacific species and approaches that of *G. multifilis* (58.9% of head length in holotype, only 2.5% in type of *micronema*, *cf*. $\bar{x}$ 59.9% for *G. multifilis*). The interoperculum is deep and nearly an equilateral triangle with only a slightly convex posterior border (Fig. 17h).

The absence of other specimens of *Gadomus* from Hawaii (apart from one listed by Gilbert, 1903:659, also from near

Kauai, but which we have been unable to locate), or from between Hawaii and the east Indies makes it impossible to tell whether the meristic and morphometric parameters overlapping those of *G. magnifilis* and *g. denticulatus* indicate inter- or intraspecific variability. On the basis of those differences that are apparent, and from its isolated locality we recognise *G. melanopterus* as a distinct species.

Table 19 Counts and measurements for the holotypes of *Gadomus melanopterus* and *G. micronema*

	melanopterus	*micronema*
D	II9	II10
Pe	18	18
Pl	9	8
GR	7+27	6+29
PC	15	12*
s-a	91.0mm	75.5mm
bd	44.5	45.6
pl	98.9	72.8 (broken)
hl	52.1	51.6
od	23.1	25.6
io	23.1	25.6
pml	58.9	60.2
pma	19.6	17.8
pms	3.5	5.0
bl	58.9	2.5**

* 9 given by Gilbert (1905)
** the length of the barbel shown in Gilbert's figure is either exaggerated or part of the barbel has since been broken off.

DISTRIBUTION. Hawaiian Islands.

DEPTH RANGE. 799–1416m.

MATERIAL EXAMINED. USNM 51606 (holotype), 91mm s-a (*ca* 270mm TL), near Kauai Island; 51643 (holotype of *Melanobranchus micronema*), 75.5mm s-a (*ca* 235mm TL) Pailolo Channel between Kauai and Molokai Islands.

Key to the Atlantic species of Gadomus

1 Outer two rays of pelvics elongated; pectoral rays 22–25 .... ***G. arcuatus***
Outer ray only of pelvic elongated; pectoral rays 18–21 .. 2

2 Gill-rakers on 1st ceratobranchial, 20–21 ...... ***G.dispar***
Gill-rakers on 1st ceratobranchial above 25 3

3 Gill-rakers on 1st ceratobranchial 25–27; pectoral fin length greater than 80% of s-a distance .... ***G.capensis***
Gill-rakers on 1st ceratobranchial 27–31; pectoral fin length less than 65% of s-a distance ...... ***G. longifilis***

Key to the Indo-Pacific species of Gadomus

1 Gill-rakers on 1st ceratobranchial 17–23 2
Gill-rakers on 1st ceratobranchial 25–29 5

2 Pectoral rays,16–18 3
Pectoral rays, 19–21 .... ***G. colletti (Japan)***

3 Interorbital width 15.5–18.0 of head length 4
Interorbital width 22.0–23.0% of head length .... ***G. intróniger*** (Philippines)

4 Gill-rakers:5–6+21–23; orbital diameter 19.8–25.6% of head length; body depth 42.0–45.0% of s-a head length .... ***G. magnifilis*** (Philippines)
Gill-rakers 4–5+17–20; orbital diameter 25.0–29.1% of head length, body depth 31.9–41.6% s-a length .... ***G. denticulatus*** (Philippines)

5 Gill-rakers 25 6
Gill rakers 27–29 ... ***G. melanopterus*** (Hawaiian Islands)

6 Barbel length 1.8–18.6% of head length; body depth 42.0–48.2% of s-a length 7
Barbel length 47.9–68.8% of head length; body depth 33.8–43.6% of s-a length ..***G. multifilis*** (Indian Ocean)

7 Barbel length 1.8–6.9% of head length; premaxillary length 57.8–60.4% of head length......... ***G. capensis*** (Atlantic ? and Indian Ocean)
Barbel length 16.6–18.6% of head length; premaxillary length 50.8–51.8% of head length........ ***G. aoteanus*** (Kermadec region)

Interspecific relationships

Interrelationships of *Bathygadus* and *Gadomus* species have not been resolved due to the paucity of osteological material. Morphometric and meristic parameters are of little use in determining such relationships, as often there is overlap. Polarity of osteological features examined such as dentition and interopercular shape are also difficult to assess. No characters suggest that the Atlantic species of either *Bathygadus* or *Gadomus* are monophyletic groups.

Among *Bathygadus* species, relatively longer jaws characterise the Japanese species (*antrodes, nipponicus*), being 51.1–72.4% head length *cf.* 48.9–61.5% in others. Interorbital width, which, in the past, has been used as an indicator of subgeneric rank is continuously variable (23.5–37.5% head length). Interopercular shape, unlike that of *Gadomus* is more varied and one group of species (*entomelas*, *filamentosus*, *antrodes*, *spongiceps*, *bowersi*) share a crook-shaped morphotype (p. 171). *Bathygadus sulcatus* and *nipponicus* also share a particular interopercular morphotype (Fig. 17, 5 & 6); these morphotypes may be indicators of relationship, but it is not possible to determine which is the derived.

Bathygadid relationships formulated by Gilbert & Hubbs (1920), and largely followed by Iwamoto (1970) and Marshall (1973*a*) are based on superficial resemblances to which polarity cannot be ascribed.

Distribution

The distributions of *Bathygadus* and *Gadomus* species coincide, both in areas occupied and numbers of species in those areas (Figs 29–32). Bathygadid specimens are few compared with other continental slope groups, eg. macrouroids, and one must guard against making too many assumptions on the basis of what are, after all, distributional plots of collecting stations. However, despite several collections from the eastern and southern Pacific and Indian Oceans (eg. Pearcy *et al.* 1982), none have yielded bathygadids suggesting that their absence from these regions is real rather than artefactual. The most significant feature of bathygadid distribution is their association with continental slopes and with 'enclosed' seas whose topography is dominated by sea-floor trenches and ridges, eg. South China, Philippine and Caribbean Seas.

Indo-west Pacific

The largest clusters of *Bathygadus* and *Gadomus* species occur in the Philippine region. Gilbert & Hubbs (1920) ascribed the large proportion of species in this area as being due to the nearly complete isolation of the Sulu Sea. This sea has particular environmental conditions, *viz.* consistently high temperature, relatively large salinity variation and lower oxygen saturation than surrounding seas. *Bathygadus* species in this region are *spongiceps* (China and Celebes Seas); *cottoides, entomelas* (Philippine Sea); *sulcatus* (Sulu Sea); *multifilis* (Celebes Sea); all at depths between 700–1600m. *Gadomus* species are *magnifilis*, *denticulatus* and *introniger*, all in the Philippine region at depths between 194–1260m.

Species from off Japan (south-east coast) are *Bathygadus antrodes* and *B. nipponicus* from depths between 792–1348m; *Gadomus colletti* from 335–1200m.

There is only one record for *Bathygadus* from the Indian Ocean; *cf. cottoides* from near Zanzibar. *Gadomus* is represented by *multifilis*, *furvescens* and *capensis*. *Gadomus furvescens* is recorded only from above the Equator (Arabian Sea and Bay of Bengal); only *G. capensis* occurs in the western Indian Ocean at lat. 40°S and along eastern Africa.

A species of each genus occurs in the Hawaiian Islands, *viz. Bathygadus bowersi* and *Gadomus melanopterus*, both from depths between 563–1440m. The occurrence of bathygadids in the Southern Ocean is also marked by a single species of each genus, *viz. Bathygadus cf. cottoides* and *Gadomus aoteanus*; both occur on Lord Howe Rise, the former also from along the Kermadec trench.

Atlantic

Six of the seven bathygadid species occurring here (*Bathygadus melanobranchus*, *B. favosus*, *B. macrops*, *Gadomus longifilis*, *G. arcuatus*, *G. dispar*) are present on both sides of the mid-Atlantic ridge. Their distribution is, however, limited to above the Equator (most northerly record, for *Bathygadus melanobranchus*, 51° 46′N; Holt & Byrne, 1908); only one species, *Gadomus capensis* occurs in the southern Atlantic. The only records for the mid-Atlantic ridge are for *Bathygadus melanobranchus*, *Gadomus longifilis* and *G. capensis* (respectively, Collett, 1896; Roule, 1919; Pakhurov, 1980). Records for the two former species are from off the Azores, and the latter from the equatorial Whale Ridge. From the western Atlantic most specimens are from the Caribbean Sea, particularly the Gulf of Mexico and from the eastern Atlantic from the Gulf of Guinea.

Merrett & Marshall (1981) commented on the narrow depth range of *Bathygadus melanobranchus* off the north-western African shelf from between 734–1017m. The depth range for Atlantic *Bathygadus* species given by Marshall (1973a) is 200–2743m and for *Gadomus* 548–2165m; only two *Bathygadus* and one *Gadomus* species are recorded from below 2000m (Fig. 28).

As noted above bathygadids appear to be absent from the eastern Pacific, an absence which may be due to a variety of factors, single or in concert such as unsuitable topography, temperature, salinity, currents affecting larval dispersal or the result of historical biogeographic events which have tied bathygadids to particular areas. Concerning the latter it is noted that a common distributional pattern occurs among other abyssal fishes, involving west-east Atlantic, high Indian Ocean, Philippines and Kermadec region (eg. Ipnopidae, various Brotulidae and Aphyonidae; Nielsen, 1965; 1966; 1969; 1977).

Discussion of bathygadid biogeography is limited by our lacking a scheme of phylogenetic relationships (p. 200), a necessary prerequisite to understanding distributional patterns.

ACKNOWLEDGEMENTS. The first author is indebted to Dr Richard Vari and the staff of the Division of Fishes, United States National Museum for their assistance and hospitality during the period of his visit which was generously funded by the Smithsonian Institution's Office of Fellowships and Grants.

We are most grateful to Dr. I. Isbrücker (Institut voor Taxonomische Zoologie, Amsterdam) and E. G. Ranchod (J. L. B. Smith Institute, Grahamstown) for loans of type specimens; to our colleagues Dr. G. Boxshall for identifying crustaceans and Ms M. Holloway for providing radiographs.

We especially thank Nigel Merrett for his advice and tolerance of our ignorance, P. Humphry Greenwood, A. Wheeler and an anonymous reviewer for their critical and helpful readings of the manuscript and to Drs Jeff Graham (Scripps Institute) and Ian Harrison (Parma University) for their helpful and stimulating discussions regarding respiration.

Finally, we express our thanks to Jennie Cummings for her word-processing and editing skills.

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Manuscript accepted for publication 30 October 1989

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6. Each table should be typed on a separate sheet designed to extend across single or double column width of a Journal page. They should have a brief specific title, be self-explanatory and supplementary to the text. Limited space in the Journal means that detailed results like locality lists, tables of measurements, details from mathematical derivations and computer print-outs will be stored in the Department of Zoology under the sectional records of the animal group concerned. These records will be considered as part of the Collections and reference should be made to them in the text.

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Bulletin British Museum (Natural History)

ZOOLOGY SERIES

Vol. 56, No. 2, October 1990